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Coastal Range and Movements of Common Bottlenose Dolphins off California and Baja California, Mexico

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Abstract.—Range and movement data from boat-based photo-identification surveys of Pacific coast common bottlenose dolphins (*Tursiops truncatus*), carried out over a 6-yr period from 1996 to 2001, were collated and analyzed. Primary data sources were from surveys carried out in four Southern California Bight study areas: Ensenada (12 surveys), San Diego (95 surveys), Santa Monica Bay (170 surveys) and Santa Barbara (61 surveys). Additional data from surveys in Monterey Bay between 1990 and 1993 (84 surveys) were also included in some analyses. Photographic matches between the San Diego, Santa Monica Bay and Santa Barbara study areas ranged from a low of 42% to a high of 67% and averaged 53%. In addition, 32 of the 58 individuals (55%) identified in Monterey Bay also occurred in one or more of the four Southern California Bight study areas. Back-and-forth inter-study area movements recorded between 1996 and 2001, were exhibited by 157 of the 246 (52%) individuals sighted in two or more study areas. Minimum travel distances ranged from 104 to 965 km, with one individual documented to have traveled from Ensenada to Monterey Bay. The most rapid travel speed was 94.5 km/day. These results reinforce earlier characterizations of coastal bottlenose dolphins being highly mobile and capable of rapid travel along the Baja California and the southern and central California Pacific coastline. It is hypothesized that these extensive movements are related to fluctuations in local, regional and perhaps Pacific-wide oceanic conditions that affect prey productivity and availability; combined with unique foraging strategies that have developed to meet these environmental fluctuations.

Bottlenose dolphins (*Tursiops truncatus*) occur as two distinct ecotypes along the California coast. The coastal form is typically found within 1 km of shore (Carretta et al.

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1998; Defran and Weller 1999; Ward 1999; Bearzi 2005) while the offshore form is distributed in deeper offshore waters, typically greater than a few kilometers from shore (Defran and Weller 1999; Bearzi et al. 2009; Carretta et al. 2013). These two ecotypes are managed by the National Marine Fisheries Service as separate population stocks (Carretta et al. 2013). Previous boat-based photo-identification surveys of coastal ecotype bottlenose dolphins within the Southern California Bight were carried out between 1981 and 1989 off San Diego, California (Hansen 1990; Defran and Weller 1999). Some surveys, using similar methodology, were also carried out in other areas off California and Baja California, Mexico, including Ensenada, Orange County and Santa Barbara (Fig. 1, Hanson and Defran 1993; Defran et al. 1999).

Abundance estimates for the coastal population, based on photo-identification surveys carried out in northern San Diego County from 1981 to 2005, estimated a population size (marked and unmarked dolphins combined) of about 450–500 (Dudzick et al. 2006; Carretta et al. 2013). Further, most individual dolphins were sighted four times or less and none appeared to be year-round or even seasonal residents of the San Diego area (Defran and Weller 1999). In contrast, some individuals in Santa Monica Bay were suggested to use that area on a seasonal basis (Bearzi et al. 2005). Additionally, a high proportion of the dolphins photo-identified in Ensenada (88%), Orange County (92%) and Santa Barbara (88%) were also sighted in San Diego (Defran et al. 1999). This inter-area overlap in sightings between widely separated study areas within the Southern California Bight explained the lack of site fidelity observed off San Diego. Further, “back and forth” travel between study areas was observed for many individual dolphins, suggesting that such inter-area movements were not a case of permanent emigration or immigration (Defran et al. 1999).

Bottlenose dolphins found in California’s coastal waters differ in their range characteristics from other well-studied populations of the species (Wells et al. 1987; Weller 1998; Maze and Würsig 1999; Krützen et al. 2004; Waring et al. 2011). Some bottlenose dolphins along the US Atlantic Seaboard, Gulf of Mexico, and western Australia use semi-enclosed bays and estuaries and commonly demonstrate high levels of site fidelity, often persistent and year-round, to these protected habitats. The range characteristics of bottlenose dolphins found in the nearshore open coastal habitats of the Atlantic and Gulf of Mexico, as well as other locations, are not well understood. However, some seasonal movements occur along the Atlantic coast and the central west coast of Florida, but the geographic extent and temporal scale of such movements are not known (Waring et al. 2011).

Subsequent to the aforementioned 1981–1989 photo-identification research by Defran et al. (1999), studies on coastal bottlenose dolphins off California were initiated in Santa Monica Bay (1997–2001) and Monterey Bay (1990–1993)¹; (Bearzi 2005). Supplementary studies extending the time-series of data for San Diego (1996–1999) were also conducted (Dudzick 1999; Lang 2002). Additional surveys were completed in Ensenada (1999–2000)² and Santa Barbara (1998–1999), where previous effort was low and the number of individuals identified relatively limited (Lang 2002) (Table 1). In combination, these new data allowed for the more comprehensive and contemporary

¹ Feinholz, D.M. 1996. Pacific coast bottlenose dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.Sc., San Jose State University, Moss Landing Marine Laboratories, Moss Landing, CA.

² Guzón-Zatarain, O.R. 2002. Distribución y Movimientos del tursiòn, *Tursiops truncatus* (Montagu, 1821) en la Bahía de Todos Santos, Baja California, México (Cetacea: Delphinidae). Master thesis, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, México.



Fig. 1. Map of California and Baja California, Mexico coastal study area locations: Ensenada, San Diego, Santa Monica Bay, Santa Barbara and Monterey Bay. Point Conception and Punta Colonet are the northern and southern coastal boundaries of the Southern California Bight.

Table 1. Summary information on survey effort, study period, photographic data, and data sources for all study areas.

Study area	Number of surveys (complete, partial)	Study period	Number of dolphins identified
Ensenada ¹	12 (12, 0)	1999–2000	81
San Diego ²	95 (48, 47)	1996–1999	292
Santa Monica Bay ³	170 (44, 126)	1997–2001	245
Santa Barbara ⁴	61 (43, 18)	1998–1999	182
Monterey Bay ⁵	84 (16, 68)	1990–1993	58

Data sources: ¹ Guzón-Zatarain, O.R. (2002). Distribución y Movimientos del tursiòn, *Tursiops truncatus* (Montagu, 1821) en la Bahía de Todos Santos, Baja California, México (Cetacea: Delphinidae). Master thesis, Facultad de Ciencias Marinas, Universidad Autonoma de Baja California, Ensenada, México; ² Dudzik (1999), ^{2,4} Lang (2002); ³ Bearzi (2005); ⁵ Feinholz, D.M. (1996). Pacific coast bottlenose dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.Sc., San Jose State University, Moss Landing Marine Laboratories, Moss Landing, CA. Some numbers differ from those given in these data sources due to refinement and revision of the dataset over time and the elimination of sightings not meeting the specified photographic quality criteria.

assessment of spatial and temporal range characteristics of California coastal bottlenose dolphins presented here.

Materials and Methods

The general design of the present study was the same as that used by Defran et al. (1999) and is similar to others studies that have carried out photo-identification catalog comparisons between independently collected data sets for a particular species (e.g., Weller et al. 2012).

Study Areas

Five distinct geographic regions along the California (San Diego, Santa Monica Bay, Santa Barbara, Monterey Bay) and Baja California, Mexico (Ensenada) coastline served as study areas (Figs. 1 & 2). While all of these study areas were generally similar, they differed from one another in the geographic extent of the coastline surveyed and in some characteristics of the nearshore topography and bathymetry (Dailey et al. 1993; Defran and Weller 1999; Defran et al. 1999; Bearzi 2005). Coastal areas surveyed were non-contiguous and ranged from Ensenada, Baja California (31°42'N, 116°40'W) in the south to Monterey Bay, California (36°58'N, 121°55'W) in the north, covering a total distance of 980 km. The locations and lengths along the coastal contour of the five study areas and the distances between their boundaries are given in Fig. 2.

Photo-Identification Surveys and Photographic Data Analysis

Similar survey methodology and photo-identification procedures were used in all study areas. Detailed descriptions of these procedures are provided elsewhere (Defran and Weller 1999; Dudzik 1999; Lang 2002; Bearzi 2005) but are briefly described here. Photographic surveys involved slow travel in small boats while moving parallel to the coast and outside the surf line; generally within 250–500 m of shore and corresponding to water depths between 4 m to 10 m (Ward 1999). Surveys were conducted in sea state and visibility conditions adequate for finding and photographing dolphins. Although past data clearly demonstrate that most coastal bottlenose dolphins are found within 500 m of



Fig. 2. Study area dimensions, coordinates and distances between study areas.

the shore (Hanson and Defran 1993; Carretta et al. 2013), two or more observers nevertheless visually searched the area from the shore to ~ 2 km offshore to ensure complete coverage of the nearshore survey strip. Once a group of dolphins was sighted, initial estimates of group size, as well as information on time, location, environmental conditions and behavior were recorded.

Following initial estimates of group size, the vessel maneuvered to a distance from the dolphins suitable for photo-identification. Using high-speed SLR cameras equipped with telephoto lenses, attempts were made to photograph every dolphin (marked and unmarked) within a group. Initial estimates of group size were revised as necessary, and contact with the group was maintained until photographic effort was completed. Identical procedures were repeated as the vessel resumed travel on the predetermined survey route and as additional dolphin groups were encountered.

In Monterey Bay and Santa Monica Bay, surveys did not always cover the entire study area. The Monterey Bay study area was divided into two sectors of approximately equal length³. Sixteen out of 84 surveys were complete and covered both sectors, while 68 were partial, covering only one sector (Table 1). In Santa Monica Bay, the study area was too large to be surveyed in one day. Thus, on a given day, surveys generally covered only the “northern” or “southern” portion of the entire study area (Bearzi 2005). When both the northern and southern portions of the study area were surveyed within several days, a complete survey was scored. Otherwise, surveys of all or only a part of the southern or northern portion of the study area were scored as partial surveys (Table 1).

Only clear photographs of dorsal fins with two or more distinctive dorsal fin notches were used for analysis. Distinctive dorsal fins were those that had sufficient notching on the trailing or leading edge such that they could be matched to high quality dorsal fin photographs from other sightings (Urian and Wells 1996; Defran and Weller 1999;

³ Feinholz, D.M. 1996. Pacific coast bottlenose dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.Sc., San Jose State University, Moss Landing Marine Laboratories, Moss Landing, CA.

Table 2. The percent of inter-study area occurrence for individuals seen in San Diego, Santa Monica Bay, and Santa Barbara (left column) with individuals seen in the Ensenada, San Diego, Santa Monica Bay and Santa Barbara comparison study areas between 1996-2001. For example: 35 of the 81 (43%) dolphins seen in Ensenada were also seen in San Diego ($n = 292$).

	Number of individuals (1996–2001)	Ensenada	San Diego	Santa Monica Bay	Santa Barbara
San Diego	292	43% (35/81)	-	58% (142/245)	67% (122/182)
Santa Monica Bay	245	22% (18/81)	49% (142/292)	-	57% (104/182)
Santa Barbara	182	9% (7/81)	42% (122/292)	42% (104/245)	-

Defran et al. 1999; Mazzoil et al. 2004). Only unambiguous matches were accepted as resightings.

Dorsal fin photographs from all study areas except Santa Monica Bay were analyzed and maintained in the Cetacean Behavior Laboratory (CBL) at San Diego State University. The photographic catalogs from Ensenada, San Diego, and Santa Barbara consisted of 397 individuals identified between 1996 and 2000, while the photographic catalog from Monterey Bay consisted of 58 individuals identified between 1990 and 1993. The Santa Monica Bay photographic catalog consisted of 245 individuals identified from 1997 to 2001. Finally, the one or two best images of each individual from the CBL and Santa Monica Bay catalogs, originally acquired in film format, were digitally scanned, and sighting histories from all six study areas were integrated into one comprehensive database.

Dorsal fin images collected in Santa Monica Bay were cross-matched to all images in the CBL catalog using techniques described in Mazzoil et al. (2004), with a few modifications. The matching process began by reviewing and verifying all previously judged matches in both catalogs. Each individual was initially assigned to category 1, 2, 3 or 4 depending on the location of the most distinctive dorsal fin notch. Then, Santa Monica Bay images were compared to all CBL images in that same category. If no match was found, the image was compared to the CBL images in all remaining categories. If a match was found, the Santa Monica Bay individual was assigned a “project number” to match the CBL individual. If no match was made between the Santa Monica Bay and CBL images, a new individual was added to the project catalog as a new “type specimen.”

Results

The primary data sources used for analysis were from surveys carried out between 1990 and 2001 in four Southern California Bight study areas: Ensenada (12 surveys), San Diego (95 surveys), Santa Monica Bay (170 surveys) and Santa Barbara (61 surveys). Additional data from surveys conducted in Monterey Bay between 1990 and 1993 (84 surveys) were included in some analyses as noted below.

Inter-Study Area Occurrence

The primary analysis of inter-study area occurrence consisted of comparisons involving the entire dataset of individual sightings ($n = 470$) acquired within the Southern California Bight study areas of Ensenada, San Diego, Santa Monica Bay and Santa Barbara between 1996–2001. An additional analysis involved a comparison of 58 dolphins identified in Monterey Bay between 1990–1993 to the 470 identified in the Southern California Bight from 1996–2001. In all cases, comparisons between study areas involved the percent of all individuals from one study area that were also sighted in another study area. For example, 35 of the 81 (43%) dolphins seen in Ensenada were also seen in San Diego (Table 2).

Thirty-two of the 58 individuals (55%) identified in Monterey Bay also occurred in one or more of the four Southern California Bight study areas between 1996 and 2001. Inter-study area occurrence of individual dolphins in the 1996–2001 Southern California Bight dataset was highest between San Diego and Santa Barbara (67%), followed by decreasing overlap between San Diego and Santa Monica Bay (58%), Ensenada and Santa Monica (22%) and finally Ensenada and Santa Barbara (9%) (Table 2).

Inter-Study Area Back-and-Forth Movements

Among the 470 dolphins identified in the combined 1996–2001 Southern California Bight catalog, 246 (52%) were sighted in two or more study areas. Of these, 157 individuals (64%) exhibited ‘back-and-forth’ movements between study areas (see also Defran et al. 1999). Back-and-forth movements were scored when a dolphin was seen in one study area (e.g., San Diego), subsequently resighted in another study area (e.g., Santa Monica Bay), and then, having apparently reversed direction, was later resighted in a study area in the opposite direction (e.g., San Diego or Ensenada). Among the 157 dolphins that exhibited back-and-forth movements, 85 individuals (54%) exhibited such 2–6 times.

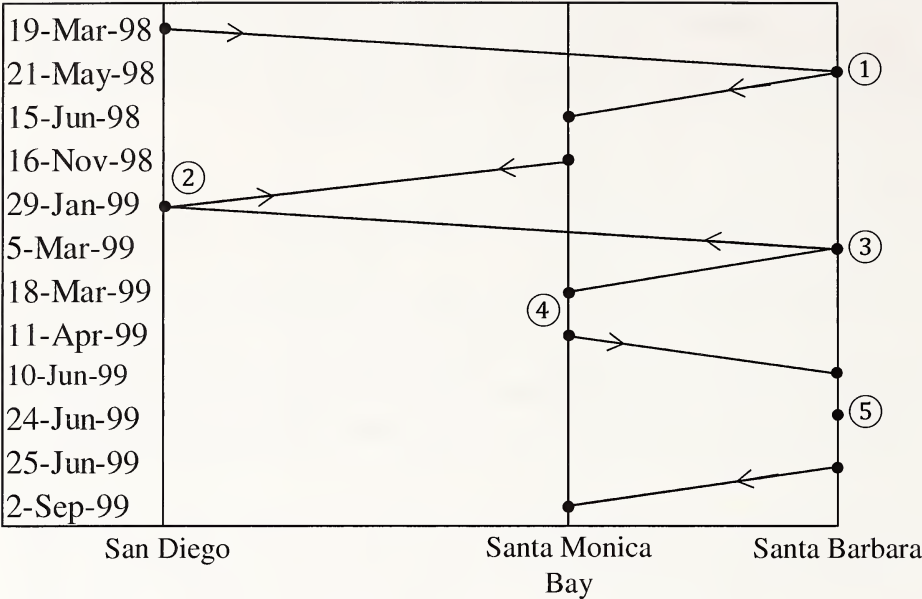
Dolphins exhibiting the most frequent back-and-forth movements in the shortest amount of time included two individuals: dolphin no. 3383 made five movement reversals within 18 months (Fig. 3A) and dolphin no. 2108 made four movement reversals within seven months (19 March 1998 to 5 October 1998). Dolphin no. 4422 (Fig. 3B) made six movement reversals, the maximum number documented, during a four-year period. Finally, dolphins exhibiting back-and-forth movements were most frequently observed in the San Diego, Santa Monica Bay, and Santa Barbara study areas, where the most surveys were conducted. Conversely, the fewest dolphins exhibiting back-and-forth movements were observed in Ensenada and Monterey Bay, where the fewest surveys were conducted.

Travel Distance and Travel Speed

For the 246 dolphins sighted in at least two study areas, the distances between their two most widely separated sighting locations were calculated (Fig. 4). The majority of these 246 dolphins (85%, $n = 209$) were documented to travel between 104 and 400 km. At the minimum, one dolphin (no. 2780) was documented to travel only 104 km from Santa Monica Bay to Santa Barbara. At the maximum, one dolphin (no. 3426) was observed in both Ensenada and Monterey Bay, a travel distance of 965 km.

Many of the surveys conducted between 1996 and 2001 in the Ensenada, San Diego, Santa Monica Bay and Santa Barbara study areas were carried out relatively close in time, which allowed for the calculation of minimum travel speeds between different locations. Three noteworthy case studies demonstrating particularly rapid travel included: (1) dolphin no. 4643 traveled 318 km from San Diego to Santa Barbara in six days (18 June to 24 June 1999), resulting in a minimum travel speed of 53 km/day; (2) dolphin no. 2221 traveled 300 km, also from San Diego to Santa Barbara, in five days (28 February to 5 March 1999), resulting in a minimum travel speed of 60 km/day; and (3) dolphin no. 3656 traveled 177 km from Santa Monica Bay to San Diego in a 12 day period (2 November to 14 November 1998), and then was sighted two days later (16 November 1998) 189 km back in Santa Monica Bay. The movement between San Diego and Santa Monica Bay in two days represents the fastest travel speed (95 km/day) recorded during the study.

3A



3B

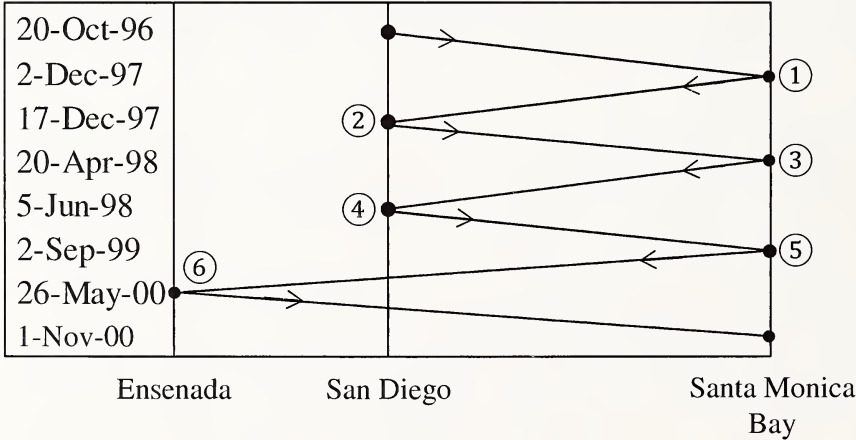


Fig. 3A. Dolphin no. 3383 exhibited five inter-study area movements between 19 March 1998 and 2 September 1999. Circled numbers indicate a direction of movement reversal and arrows represent the direction of travel. Fig 3B. Dolphin no. 4422 exhibited six reversals between 20 October 1996 and 1 November 2000.

Discussion

Range and Movement Comparisons

The movements of coastal bottlenose dolphins reported herein were generally similar to results from an earlier study on the range and movement characteristics of this population between 1981–1989 (Defran et al. 1999). In that study, dolphins showed a

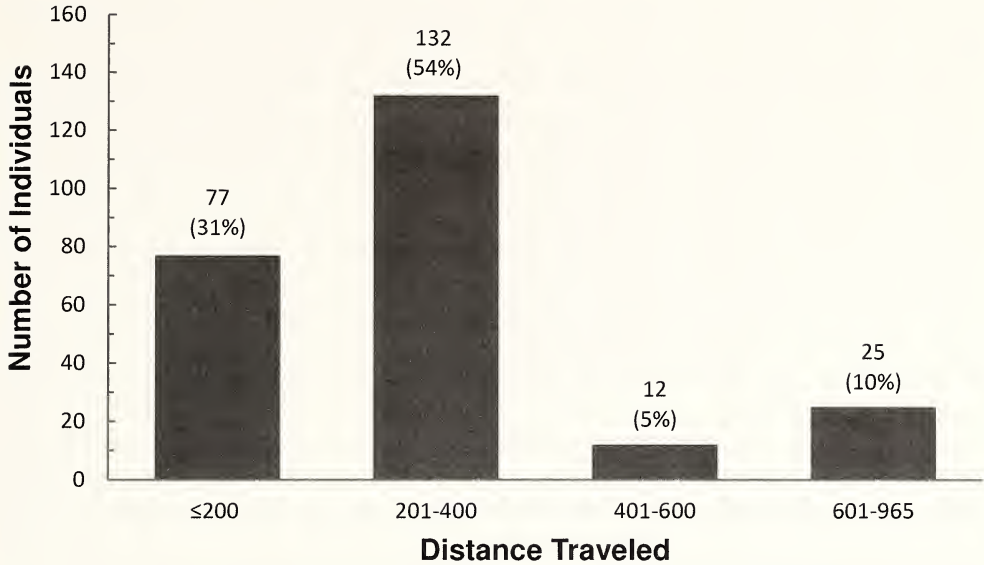


Fig. 4. Minimum estimates of distances traveled for 246 identified dolphins that were sighted two or more times between 1996 and 2001.

high degree of travel between San Diego and other study areas in the Southern California Bight, displayed regular inter-study area back-and-forth movements, and exhibited relatively rapid travel over extensive coastal distances. The most notable difference between the current results and those reported by Defran et al. (1999) was the somewhat lower percent of resighting overlap between the Southern California Bight study areas. For example, Defran et al. (1999) reported that between 88% and 92% of the dolphins identified in Santa Barbara, Ensenada and Orange County were resighted in San Diego (1981–1989 dataset). In the current study, inter-study area overlap between San Diego, Santa Monica and Santa Barbara ranged from 42% to 67% during the 1996–2001 study period. Overlap between Ensenada and the other study areas in the Southern California Bight between 1996 and 2001 was even lower, ranging from 9% to 43% (Table 2).

The causal mechanisms driving the lower levels of overlap between the Southern California Bight study areas is unresolved, but available information provides some support for the concept of coastal dolphins progressively expanding use of more northern portions of their range. Prior to the powerful 1982–83 El Niño, the presumed northern range limit for these dolphins was Pt. Conception. Subsequent to the 1982–83 El Niño, there were an increasing number of coastal dolphin sightings documented along the coastline from Pt. Conception to Monterey Bay (Table 1 in Wells et al. 1990). One of the earliest of these sightings was off the coast of Santa Cruz, CA. Photo-identification images from that sighting showed that nine of these dolphins had previously been identified off San Diego between 1981–1983 (Hansen 1990). Continued photo-identification studies carried out on dolphins in Monterey Bay between 1990–1993 confirmed that 55% of the dolphins identified there had previously been identified between 1981–1989 within the Southern California Bight (Hansen 1990; Defran and Weller 1999; Defran et al. 1999; this report). The nearly continuous presence of bottlenose dolphins in the Monterey Bay area from 1990 to the present indicates that the range extension described by Wells et al. (1990) has persisted (e.g., Riggins and

Maldini 2010; Maldini et al. 2010), and in fact, has further expanded into San Francisco Bay⁴.

While these hypothesized changes in the northern distribution of the species seem plausible, it is less likely that similar changes were occurring to the south (e.g., Ensenada study area). That is, a shift (increase) in habitat use to the south would seemingly have resulted in higher inter-area resightings for Ensenada than those reported here (Table 2). Further support for an increased presence of coastal bottlenose dolphins in the northern portion of their range comes from the number of dolphins identified there. Over 300 coastal dolphins were photographically identified in Monterey Bay from 1990 to 2010 (Maldini et al. 2010) and 67 off Santa Barbara between 2009 and 2010. Interestingly, of the 67 dolphins identified off Santa Barbara, 31 (46%) have also been sighted in Monterey Bay⁵, demonstrating a considerable amount of interchange between these two northern study areas.

It is also possible that increased research effort has contributed to more precise estimates of inter-study area occurrence. That is, survey effort, as well as the number of dolphins identified, especially in Ensenada and Santa Barbara, was considerably higher for the 1996–2001 dataset than it was for the 1981–1989 dataset. Further, the survey distance covered during Santa Monica Bay surveys (conducted only during 1997–2001) was considerably greater than that covered in other study areas. Taken together, the sample values used for assessing inter-area overlap during 1996–2001 may reflect the influence of greater effort, and thus may be more precise than the 1981–1989 dataset. The impact of regional and global oceanic events and trends such as El Niño, which occurred during and in close proximity to both the 1981–1989 and 1996–2001 sample periods, may have also played a role in the greater inter-area overlap observed in the 1981–1989 dataset. While this speculation about differences between the two datasets may be plausible, an alternative explanation is that lower inter-area overlap in the 1996–2001 dataset (compared to the 1981–1989 dataset) reflects a change in range characteristics for some individuals.

The range and movement patterns described herein, including those from Defran et al. (1999), are probably quite conservative estimates of these processes. By way of illustration, surveys within the six study areas (i.e., Ensenada, San Diego, Orange County, Santa Monica Bay, Santa Barbara and Monterey Bay) cover only 262 km of the 980 km coastline (extending from Ensenada to Monterey Bay). Further, even for the most contemporary research effort (1996–2001), surveys were carried out on only a very small percent of the 1,460 possible days in any study area. Therefore, our descriptions of the frequency and geographic scope of coastal bottlenose dolphin movement patterns are a byproduct of sampling effort.

Range and Movements Interpretation

Most interpretations of the spatial and temporal range characteristics of California coastal bottlenose dolphins have emphasized the primary role played by the nearshore distribution and abundance of dolphin prey (Weller 1991; Defran et al. 1999; Dudzik

⁴ Szczepaniak, I., W. Keener, M. Webber, J. Stern, D. Maldini, M. Cotter, R.H. Defran, M. Rice, G. Campbell, A. Debich, A. Lang, D. Kelly, A. Kesaris, M. Bearzi, K. Causey, and D. Weller. 2013. Bottlenose dolphins return to San Francisco Bay. Paper presented at the 20th Biennial Conference on the Biology of Marine Mammals, Dunedin, New Zealand December 9–13.

⁵ Frohoff, T., L.D. Griffin, M.P. Cotter, and D. Maldini. 2010. California coastal bottlenose dolphin population in Santa Barbara relative to Monterey Bay: preliminary findings. Retrieved June 23, 2012 from www.protectourdolphins.com/uploads/ACS_Poster-_FINAL_VERSION.pdf.

1999; Ward 1999; Lang 2002; Bearzi 2005). Dynamic variations in oceanic processes such as El Niño and La Niña, regional processes such as upwelling and variable expressions of the California Current System, and local substrate and habitat effects, are all presumed to play a critical role in prey availability.

The most integrated interpretation of the extensive coastal movements demonstrated by these dolphins stresses the interplay between environmental variables, prey item preferences and distributional characteristics, as well as behavioral repertoires and distinctive foraging strategies (Defran et al. 1999). While preferred prey items for Pacific coast bottlenose dolphins, such as surfperch (Embiotoridae) and croakers (Sciaenidae) are widely distributed along the eastern Pacific coastline, their abundance and distribution is unpredictable and patchy. An apparent and recurrent foraging response to this unpredictable distribution of prey is a pattern of movement within the nearshore zone referred to as “localized” and “directional” movement (Ogle 2005). During localized movement, dolphins move back-and-forth along shore in a restricted area, often of several kilometers or less. During directional movement, dolphins travel in the same direction, north or south, and parallel to the coast. When these movement types were compared, significantly more feeding occurred during localized movement and significantly more travel occurred during directional movement. In this case, localized movement was hypothesized to be foraging behavior related to a prey patch.

In light of the extensive longshore movements reported herein, we suggest that coastal bottlenose dolphins off California and Mexico are moving great distances in search of preferred but unpredictable nearshore prey patches. Once a prey patch is located, longshore directional travel (movement between patches) ceases and localized movement (movement within patches) commences. As local prey patches become depleted or are effectively ‘fished,’ dolphins “relocate” in search of more optimal conditions (Defran et al. 1999). This relocation strategy manifests itself in the type of inter-study area movements found during the current study.

Conclusions

The results presented here reinforce and extend earlier characterizations of coastal bottlenose dolphins being highly mobile along the central and southern California and Baja California coastline. More specifically, dolphins in this population routinely move distances of several hundred kilometers or more along the coastline. These extensive movements are thought to vary with fluctuations in local, regional, and perhaps Pacific-wide oceanic conditions which affect prey productivity and availability. In the extreme, dolphin groups alternate between back-and-forth movements over small stretches of coastline (several kilometers) while foraging on concentrations of preferred prey. When these prey concentrations are diminished, dolphins travel parallel to the coast, north or south, until they encounter another prey patch. Although many of the dolphins identified in this study were observed to use extensive coastal ranges, it is uncertain if some individuals use more limited core ranges. The small size of the coastal bottlenose dolphin population (<500) in combination with its affinity for very nearshore waters make them vulnerable to a number of human related threats including fishery-related mortality, pollution from coastal runoff and habitat degradation resulting from urbanization. Knowing that a substantial portion of this population moves along a nearly 1000 km long stretch of the coastline, including trans-boundary movements into Mexico, is of particular value to management objectives, particularly with respect to understanding potential risks to their survival.

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Status and Trends in the Southern California Spiny Lobster Fishery and Population: 1980–2011

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Abstract.—The California spiny lobster (*Panulirus interruptus*) fishery in southern California ranks amongst the State’s most economically important fisheries. An analysis of commercial harvest data confirms that the fishery was landing near-record catches in the late-2000s through early-2010s. Advances in recreational fishing technology likely tempered commercial fishery landings per unit effort. The commercial catch per trap pulled declined 15%, on average, in years after the introduction of a new rigid-style hoop net in the recreational fishery. Fishery-independent data sourced from power plant marine life monitoring recorded increased California spiny lobster abundance after 1989 with evidence of increased larval settlement beginning circa 1989. This timing was consistent with previously reported oceanographic changes in the North Pacific. Abundance indices for lobsters likely one-year’s growth away from recruiting into the fishery and the young-of-the-year, both derived from power plant abundance records, significantly predicted the commercial landings at index-appropriate temporal lags, i.e. one year for next year’s recruitment. Carapace lengths measured during power plant surveys in Santa Monica Bay, where commercial fishing was prohibited, significantly declined for the total sample and females only after the introduction of the new rigid hoop net. Male carapace lengths were not significantly different between the two periods. The power plant data confirms that, as of 2012, the fishery appears healthy but warns of the need to monitor sublegal individuals and their dependence on oceanographic conditions. These analyses also indicate the urgency of monitoring the recreational fishery harvest, especially the potential effects of the new rigid hoop net.

Exploitation of spiny lobsters (Family Palinuridae) occurs worldwide. These fisheries rank among the most economically valuable in their respective regions (Phillips 2006; Lipcius and Eggleston 2008). Historically, substantial research was directed at understanding spiny lobster population variability (Polovina et al., 1995; Lipcius and Eggleston 2008) and predicting future fishery success by examining abundance indices of pre-recruitment size classes (Cruz et al., 1995; Cruz and Adriano 2001). These data commonly resulted in stock assessments and fishery management plans designed to maintain sustainable fisheries (Phillips et al., 2010). Despite its importance to California’s marine fisheries, California spiny lobster (*Panulirus interruptus*) historically received little research within California waters (Mitchell et al., 1969; Pringle 1986; Barsky 2001) in comparison to other spiny lobster fisheries worldwide. Recently, however, increased effort has been applied to understanding California spiny lobster biology, ecology, and fisheries (Arteaga-Rios et al., 2007; Mai and Hovel 2007; Parnell et al., 2007; Neilson and Buck 2008; Neilson et al., 2009; Koslow et al., 2012; Selkoe et al., 2010; Withy-Allen 2010; Miller et al., 2011a; Neilson 2011; Kay et al., 2012a; Kay et al., 2012b).

Table 1. Summary of existing (as of December 2012) California spiny lobster recreational and commercial fishing regulations in California.

Regulation	Fishery	
	Recreational	Commercial
Minimum Size	82.5 mm CL	
Seasonal Closure	Mid-March through September	
Permit Needed	Fishing License	Limited-Entry
Bag Limit	7 individuals	None
Capture Method	Diving by hand, Hoop Net	Trap
Catch Reporting	Report Card	Logbook
Mini-Season	5 days	NA

California spiny lobster (hereafter lobster) was commercially fished since the 1800s (Neilson 2011) with recreational or subsistence fishing likely as long. The commercial fishery peaked during the post-World War II years through the mid-1950s when the numbers of immature lobsters taken was recognized and accounted for in new regulations (Neilson 2011). Regulation changes between 1957 and 1976 reduced the catch of smaller, sublegal lobsters. Landings again increased in the late 1980s reaching a plateau of approximately 250 metric tons annually in the mid- to late-2000s (Neilson 2011; Koslow et al., 2012).

Recreational harvesting of marine species was long considered inconsequential in comparison to commercial landings, but recent evidence suggests otherwise (Eggleston et al., 2003; Coleman et al., 2004; Birkeland and Dayton 2005; Erisman et al., 2011). The southern California recreational lobster fishery landings over time are unknown and likely varied in response to lobster population abundances, angler participation rates, and advances in fishing technology. Minimal information on historic recreational catch and participation exists. The introduction of a lobster report card issued by the California Department of Fish and Wildlife (DFW) in 2008 may alleviate this problem in the future, but the lack of historic data hampers present analyses. This lack of information confounds understanding the population’s health, in the absence of fishery-independent data, considering the recreational catch was estimated at 30–60% of the commercial catch (Neilson 2011).

The two lobster fisheries in California were governed by a suite of similar regulations but also fishery-specific rules (Table 1). Equipment used in each fishery bore relevance to this discussion. Traps were the only technology available to commercial fishers. Regulations governing their design remained unchanged since 1976. Market demand resulted in the commercial fishery targeting smaller individuals by utilizing smaller entrance funnels on each trap resulting in minimal variation in the harvested size since the 1980s (Neilson 2011; Barsky 2012; Healy 2012). In contrast, the recreational fishery targets all legal size classes, often prizing larger individuals (Neilson 2011). Recreational scuba divers once dominated the fishery with comparatively minor harvests by hoop net anglers (Neilson et al., 2009). This changed recently, coinciding with the introduction of a new rigid, conical hoop net (new hoop net) in 2006 (Tackletour 2006). More lobsters were landed per hoop net set using the new hoop net in comparison to the traditional hoop net (Neilson et al., 2009) thus raising concerns regarding their potential impact on the population if extensively adopted by the recreational fishery. Past experiences in other spiny lobster fisheries suggest this concern may be warranted. Recreational-only fishing periods used in Florida, similar to those used in California, resulted in significant

reductions in Caribbean spiny lobster (*Panulirus argus*) population density when pre-recreational season and pre-commercial season surveys were compared (Eggleston et al., 2003). Similar surveys have thus far not been completed in California.

To enhance management strategies, California resource managers recently completed a stock assessment despite limited fishery-independent population data (Neilson 2011) a noted shortcoming in the assessment (Cope et al., 2011). The lack of annual recruitment estimates and overall year class strength indices were highlighted as significant data gaps. Prior attempts to fill these gaps utilized historic plankton tows offshore off California (Pringle 1986; Koslow et al., 2012). Their results were informative of gross changes in population abundances, but inconclusive in explaining the interannual variation in lobster landings. Planktonic stage abundance indices often fail to predict future fishery patterns due to the variety of mortality sources acting on larval and pre-recruit stages (Houde 2008).

Coastal power plant marine life entrapment monitoring programs were found to provide previously unused data supporting fisheries analyses (Field et al., 2010; Erisman et al., 2011; Miller et al., 2011b; Miller and McGowan 2013). Invertebrate records were never evaluated, but hold promise as a fishery-independent data source. Furthermore, three monitored power plants were situated in the Santa Monica Bay, California where commercial lobster fishing was prohibited, but recreational fishing was permitted. Using these data, this work aims to investigate important concepts regarding the California spiny lobster population that directly affects the fishery's management. The primary purpose of this investigation is two-fold. First: fill knowledge gaps related to population abundance cycles over time; recruitment patterns and their relationship with the fishery landings; and interannual variability in larval settlement patterns. Second, use these compiled data to test the hypothesis that the lobster population and commercial fishery have changed in measurable ways since the introduction of the new hoop net.

Material and Methods

Data Sources

Total annual commercial landings, in metric tons (MT), were compiled from Perry et al., (2010) for all DFW fishing blocks in southern California. Fishing blocks represented a designated spatial grid of 10-minute latitude $\times$ 10-minute longitude numbered areas, except along the coast where the coastline bounds the area and reduces the fishing block's overall size. Data was screened to remove those landings reported from fishing blocks encompassing bathymetry exceeding the lobster's known maximum depth (73 m; Barsky 2001) and accounted for $< 1\%$ of the total cumulative landings, 1980–2008. Spatial distribution of the total harvest (1980–2008 cumulative) was visualized using ArcGIS 10 with five natural breaks segregating the data.

Fishery-independent lobster data collected during power plant monitoring records as described by Miller and McGowan (2013) were compiled. Of the five power plants examined (Figure 1), three had intakes surrounded by soft-bottom sandy habitat where the intake structures themselves represented one of the few high-relief substrates in the area (Table 2). These were Scattergood Generating Station (SGS), El Segundo Generating Station (ESGS), and Huntington Beach Generating Station (HBGS). The primary Redondo Beach Generating Station (RBGS) intake was located near the King Harbor breakwall, a well documented mature artificial reef (Stephens et al., 1994). Lastly,

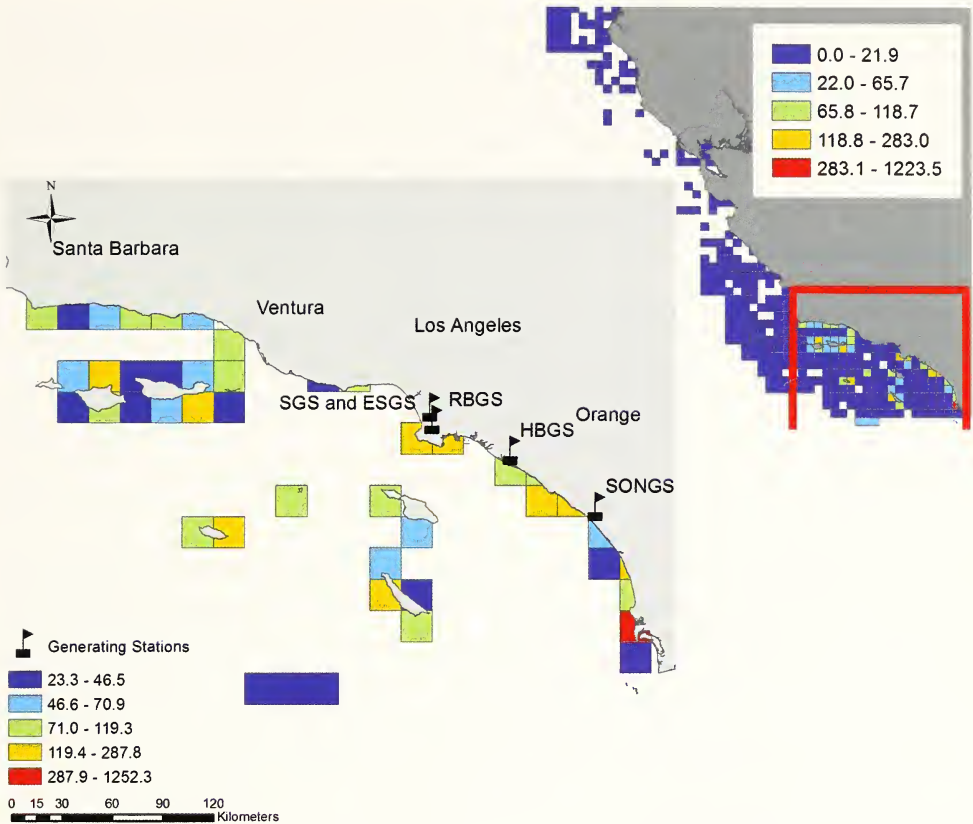


Fig. 1. Total metric tons, based on landings, harvested from each California Department of Fish and Game fishing block, 1980–2008 commercial California spiny lobster seasons (October - March). The upper map depicts all Southern California Bight fishing blocks where lobster have reportedly been taken. The lower map depicts only those fishing blocks contributing > 1% of the total commercial landings, 1980–2008. Location of the four power plants used in this analysis is presented. They are San Onofre Nuclear Generating Station (SONGS), Huntington Beach Generating Station (HBGS), Redondo Beach Generating Station (RBGS), El Segundo Generating Station (ESGS), and Scattergood Generating Station (SGS). Scattergood and El Segundo are less than 3 km apart from each other with Scattergood upcoast from El Segundo.

San Onofre Nuclear Generating Station’s (SONGS) intakes were situated adjacent to or in a cobble stone reef with a large kelp forest.

At each power plant, the intake conduit emptied into a sedimentation basin (or forebay) within the power plant property. This reduces the overall water velocity and allows animals, such as fish and invertebrates, to take up residence within the forebay. Perpendicular to the conduit bulkhead lie steel mesh traveling screens designed to prevent large material from passing further into the cooling water system. Traveling screen mesh was 10-mm square mesh. At the discretion of power plant operators, a heat treatment was conducted to control biofouling growth within the cooling water system. This resulted in a forebay water temperature > 35°C for a minimum of one hour. During this time the traveling screens operated continuously removing all stressed and moribund marine life from the forebay. All material (marine life and debris) within the forebay became impinged upon the traveling screens, was carried out of the forebay, and washed off into

Table 2. Descriptive parameters for each power plant cooling water system monitored and supplying data on California spiny lobster abundance. Mean flow refers to the volume of cooling water circulated between heat treatments. Median carapace length (CL mm) and standard error for California spiny lobsters measured during surveys since 1993.

Parameter	Scattergood	El Segundo	Redondo Beach	Huntington Beach	San Onofre
# of Intakes	1	2	2	1	3
Intake Depth (m)	9.0	9.8	13.7	27.5	9.1
Riser Height (m)	3.2	3.0	3.0	2.4	2.9
Distance Offshore (m)	488	698	289	457	960
Habitat Surrounding Intake	Sand	Sand	Reef	Sand	Reef, Kelp
# of Surveys	100	208	277	192	272
Mean Flow (10^6 m ³) (SE)	273.8 (98.9)	66.1 (4.4)	87.6 (3.9)	59.7 (3.2)	168.5 (47.1)
Years Surveyed	1993–11	1980–10	1980–06	1980–98, 2001–10	1980–93, 2006–07
Median CL (mm)	76	79	72	13	66
Standard Error	0.45	0.81	0.35	0.97	1.35

a collection basket. At the end of the heat treatment, few, if any, animals remained within the forebay. Lobsters impinged during heat treatments were counted, batch-weighed, and measured to the nearest mm CL (beginning in 1993). The cooling water flow volumes between heat treatments were compiled from power plant records of daily cooling water circulated. Environmental data included the following indices: Pacific Decadal Oscillation (PDO; Mantua et al. 1997), North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008), Multivariate ENSO Index (MEI; Wolter and Timlin 2012), and daily seawater temperature at 5 m (BST) recorded at the Scripps Institution of Oceanography (UCSD 2012).

Data Analysis

Fishing effort data was unavailable prior to 1997, therefore annual landings were presented unstandardized to effort. Both effort and landings data were provided by the DFW for the 2000–2010 fishing seasons (ca. October - March). Using these data, a catch per unit effort (CPUE; legal lobster count/trap pulled) was derived. Their use was limited due to the brevity of the CPUE series in comparison to the other data sets evaluated. The CPUE series was used to compare pre- and post-introduction of the new hoop net to investigate possible changes in the commercial fishery that could be attributed to the new recreational fishing technology. Comparisons were made using a Kruskal-Wallis test.

Lobster abundance and biomass data collected during power plant monitoring were standardized to circulated cooling water volumes to account for variation between plants and daily operations over time. The resulting entrapment rate (ER; count/ 10^6 m³) was used in subsequent analyses. Trends were tested for significance (meaningfulness) using a MS Excel add-in wherein the lobster time series was broken into intervals of varying length before analyzed using linear regression (Bryhn and Dimberg 2011). Individual weights were not recorded during surveys; therefore a mean individual weight was derived by dividing the aggregate biomass by the total count. This supplemented the size information collected after 1992. Median carapace lengths were calculated for lobsters measured at each power plant to indicate the size structure sampled. The annual median length (total, female, and male) from lobsters collected at SGS was examined for changes in the overall size structure with time at a location free of commercial fishing pressure.

Sampling dates were matched to years corresponding to the fishing seasons and intervening period before the next season, i.e. October 1 - September 30. For example, data collected from October 1, 2009 - September 30, 2010 was included in the 2009 annual median length. This analysis was limited to SGS as it was the only power plant meeting two criteria: 1) located in the Santa Monica Bay where commercial fishing was disallowed, 2) robust sample size in years before and after the new hoop net introduction. The remaining power plants did not meet both of these criteria (Table 2). A Kolmogorov-Smirnov test was used to compare lengths from the two periods, pre- and post-new hoop net.

Individuals between 72.5 and 81.5 mm CL were assumed to represent new fishery recruits the following year. Their abundance by heat treatment was standardized consistent with the ER technique to derive the next-year's-fishery-index (NYFI; count/ 10^9 m^3). Assuming commercial landings predominantly represent first-year recruits (Neilson 2011), landings were plotted as a function of the NYFI after advancing the index one year. Individuals measuring less than 21 mm CL were assumed to be young-of-the-year. From their survey-specific abundance, a young-of-the-year index (YOYI, count/ 10^9 m^3) was derived following the same methods described for the ER and NYFI. Environmental indices were compared with the YOYI to examine the potential relationship between the environment, as measured by the indices, and lobster settlement using a Spearman's rank correlation. When identified, autocorrelation was addressed by adjusting the r_{crit} using the modified Chelton method (Pyper and Peterman 1998). All statistical analyses, other than the power plant trend analysis, were completed in R (R Development Core Team 2012).

Results

California Department of Fish and Wildlife records indicate lobster has been taken commercially across a wide portion of the California coastline (Figure 1). The majority of fishing blocks contributed less than 22 MT of landed lobster during the 29 years reviewed. These areas were excluded and the remaining analyses focused on the 43 fishing blocks supporting the bulk of the commercial fishery. Landings from the southern portion of the area were generally higher than those farther north (Figures 1 and 2a), including the peak along Point Loma in San Diego, California. Additional areas producing high biomass landings included rocky headlands at Dana Point and Palos Verdes along the mainland, and at San Clemente, San Nicholas, Santa Cruz, and Santa Rosa Islands.

A shift in the early 1990s indicated increased landings from areas outside of San Diego County (fishing block series 800). The mean seasonal percentage of the total landings prior to 1994 in the southernmost fishing blocks accounted for 55% but declined to 45%, on average, through 2008 (Figure 2b). During this 1994–2008 period, landings in the 700-series fishing blocks offshore of Los Angeles and Orange Counties increased by only 2%, on average, from their 1980–1993 mean. Landings from the 600-series fishing blocks offshore of Santa Barbara and Ventura Counties increased 8% during the latter 15 years in comparison to the 1980–1993 period.

Commercial landings from these 43 blocks initially declined to a minimal level (<150 MT/annually) in the 1980s before increasing to relatively consistent annual landings of approximately 250 MT since 2000 (Figure 3a). Since 2000, the mean annual CPUE has remained > 0.36 legal lobsters/trap and ranged as high 0.54 legal lobsters/trap (Figure 3b). Prior to the introduction of the new hoop nets in the recreational fishery,

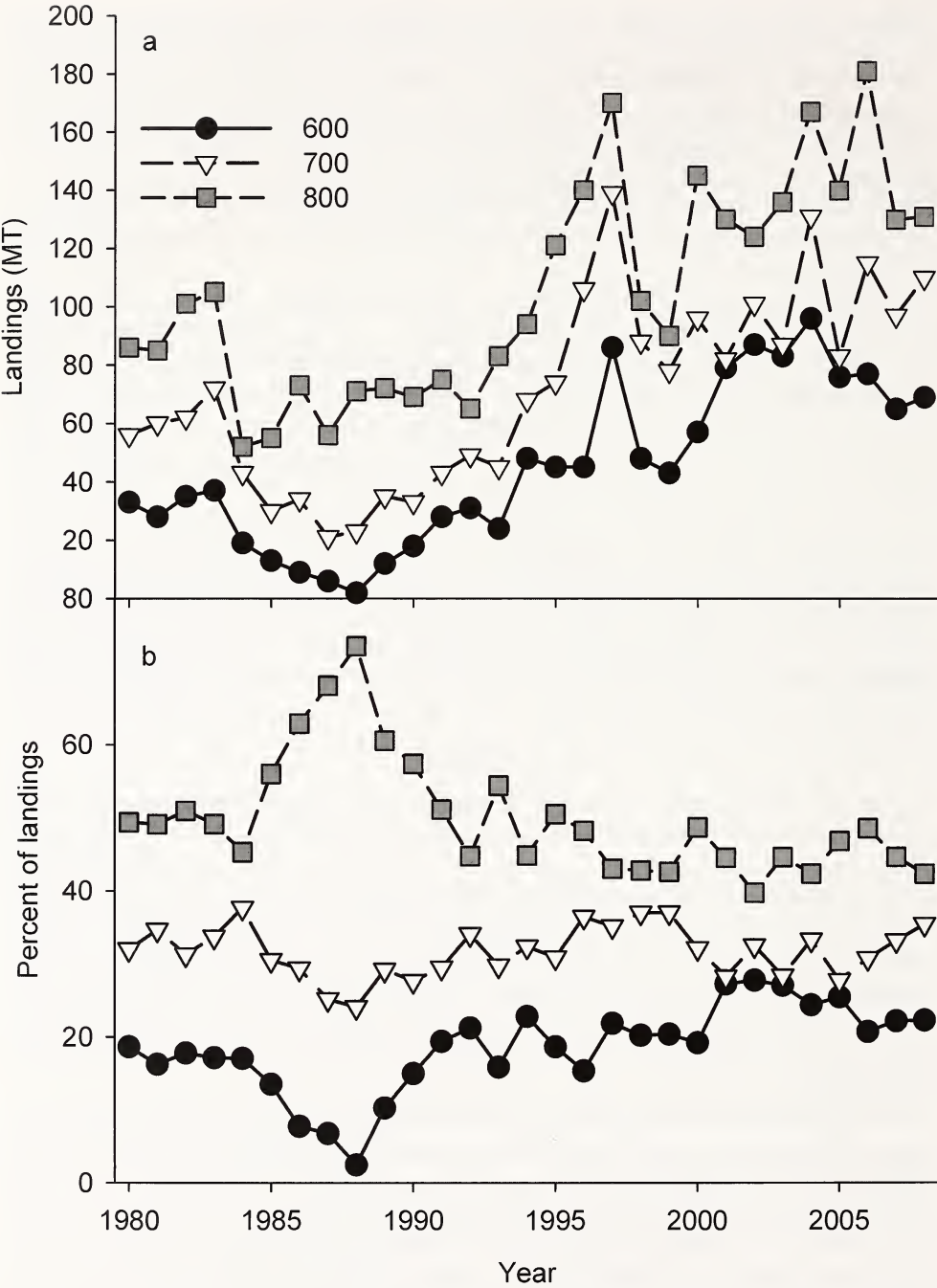


Fig. 2. a) Total California spiny lobster landings (metric tons, MT) by fishing block series and fishing season; b) percent of landings by fishing block series. Block series: 600 = Santa Barbara and Ventura Counties, California; 700 = Los Angeles and Orange Counties; 800 = San Diego County.

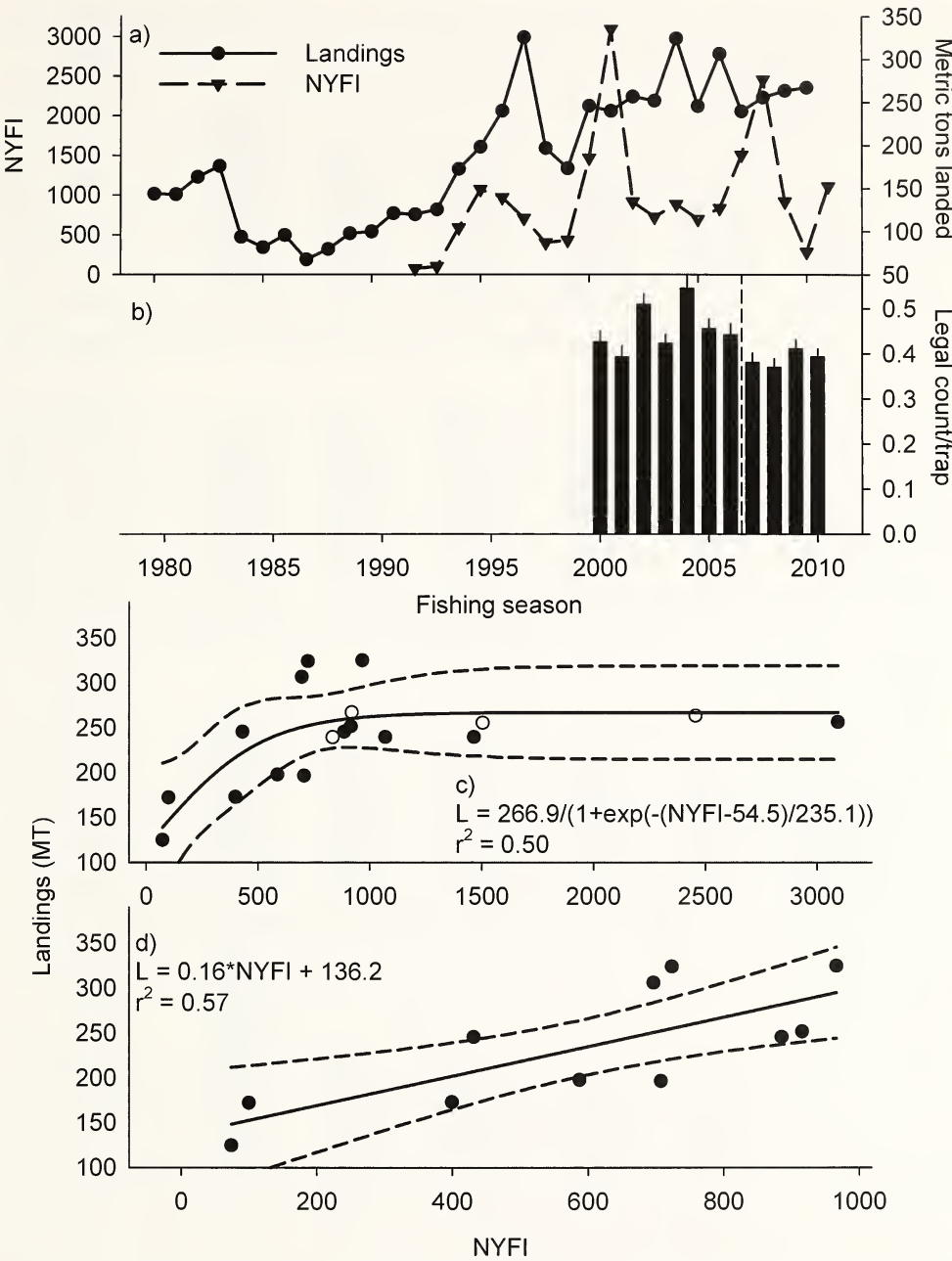


Fig. 3. a) Commercial California spiny lobster landings from those fishing blocks contributing $\geq 1\%$ of the total commercial landings, 1980–2008. The next-year's-fishery-index (NYFI; count/ 10^9 m^3) by year derived from power plant entrapment surveys (1992–2011). b) Commercial fishery catch per unit effort (legal count/trap pulled) for the same fishing blocks used for a). c) Total landings (1993–2010) plotted as a function of the NYFI after adjusting for a one-year lag. White circles indicate those seasons since the introduction of a rigid-style hoop net in the recreational fishery (2007–2010). A sigmoidal function best described the distribution ($r^2 = 0.50$). Dashed lines indicate 95% confidence intervals. d) Subsampling data from figure 3c for just NYFI $< 1000/10^9 \text{ m}^3$, or the asymptote threshold indicated in figure 3c resulted in greater predictability ($r^2 = 0.57$). Dashed lines indicate 95% confidence intervals.

the commercial CPUE averaged 0.46 legal lobster/trap. After the 2006 introduction, this declined to 0.39 legal lobster/trap, or a significant 15% reduction (KW, $\chi = 3.98$, $df = 1$, $p = 0.046$). Interannual CPUE variability declined after the 2006 season as the coefficient of variation declined from 1.00 prior to 2007 to 0.89 after 2006. Changes in the CPUE at the onset of this introduction were prominent across the Southern California Bight with mean monthly CPUE across all block series lower after the introduction, with one exception (Figure 4). The disparity between the two periods was generally higher during the first one-half of the season in all areas (Figure 4 b–d). In the San Diego area (fishing blocks numbered 801–899), the disparity was greatest during the first three months and waned thereafter, with post-introduction February CPUE slightly exceeding the pre-introduction mean. This was the only instance of the post-introduction period exceeding the pre-introduction mean.

Trends in the fishery-independent population indices at each power plant were independent of each other with some exceptions (Figure 5). Entrapment rate trends at SGS significantly correlated with both ESGS ($r = 0.58$, $p = 0.01$, $n = 18$) and HBGS ($r = 0.63$, $p < 0.01$, $n = 17$). No correlation existed between the ESGS and HBGS trends. Trends at RBGS and SONGS were not correlated with any other power plant. Where data were available, an overall increasing trend in lobster population abundance (higher ER) was recorded beginning in the late-1980s, (Figure 5a). Monthly ER averaged over the entire series indicated general peak abundance in late-summer to early-fall period at each power plant (Figure 6). The ER at RBGS was the lone exception as it peaked in spring.

Three power plants in Santa Monica Bay recorded data from an area free from commercial fishing pressure. At SGS, the farthest north of the three Santa Monica Bay power plants, lobster data was available beginning in 1993, from which a meaningful increase in ER was observed through 2011 ($r^2 = 0.51$, $p < 0.001$), excluding a brief depression in 2005 (Figure 5b). The SGS data were dominated by lobsters near the legal size limit (Table 1). Length measurements recorded at SGS were available from every year, 1998–2011. This was the only Santa Monica Bay power plant length series sufficiently spanning 2006 when the new hoop nets were introduced. Lobster carapace lengths pre-introduction were significantly larger than post-introduction across all samples (KS, $D = 0.0998$, $p < 0.001$; Figure 7a) and for females (KS, $D = 0.1323$, $p < 0.001$; Figure 7b), but not for males (KS, $D = 0.0705$, $p = 0.10$; Figure 7b). At nearby ESGS, the ER was more variable than at SGS and extended to 1980 (Figure 5c). Lacking any significant trend, generally higher ERs were observed at ESGS in the last decade than during the preceding two. Most lobsters taken at ESGS were also near the fishery's minimum size with the largest median CL recorded. Average weight of lobsters taken at ESGS was more variable prior to 1993, with a fairly stable mean weight of 500g during the 1993–2008 period before declining in later years. At the southeast edge of the Santa Monica Bay, RBGS also commonly entrapped lobsters with no significant trend detected, but declining cooling water use by RBGS reduced the need for heat treatments (Figure 5d). Therefore, the usable time series ended in 2006. Entrapment rates at RBGS were also predominantly reflective of lobsters near recruiting to the fishery. Mean biomass of lobsters entrapped prior to 1990 were 80 g larger than after, suggesting an increased influence of smaller individuals since 1990.

Huntington Beach Generating Station entraps few lobsters in comparison to the Santa Monica Bay power plants, and as with prior examples, a statistically insignificant abundance trend was observed (Figure 5e). In 1989, and several years after, the ER

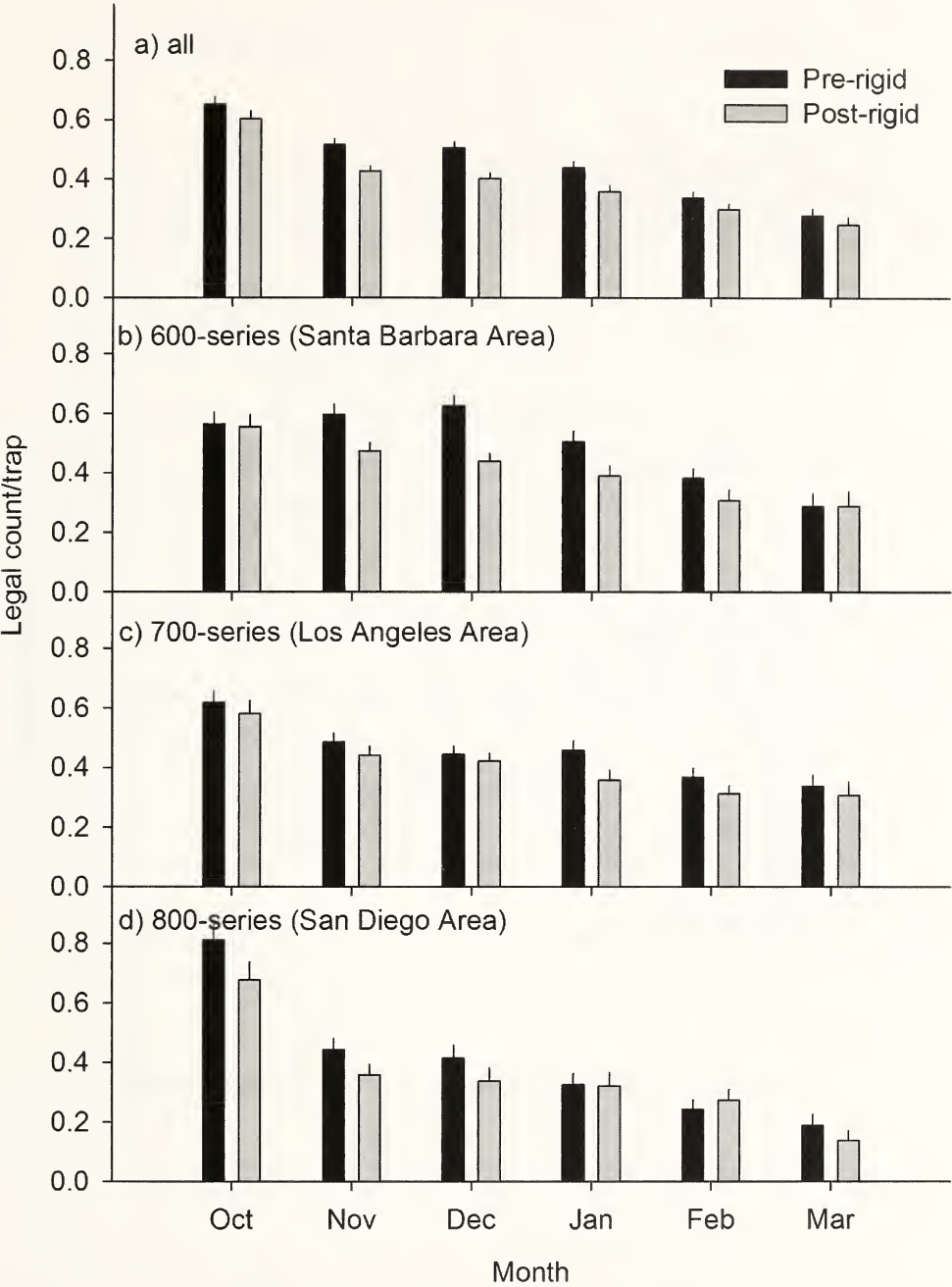


Fig. 4. Mean monthly commercial California spiny lobster catch per unit effort ($\pm$ s.e.) before (2000–2006) and after (2007–2010) the introduction of the rigid-style hoop net for recreational fishers a) across all fishing blocks in the 600–800 series, b) 600-series blocks, c) 700-series blocks, d) 800-series blocks.

periodically increased substantially as a comparatively large number of lobsters were taken. Excluding 1989, the mean HBGS ER after 1989 was nearly four times greater than was recorded prior to 1989. Unlike the three Santa Monica Bay power plants, lobsters taken at HBGS were considerably smaller with a median CL of 13 mm (Table 2). This

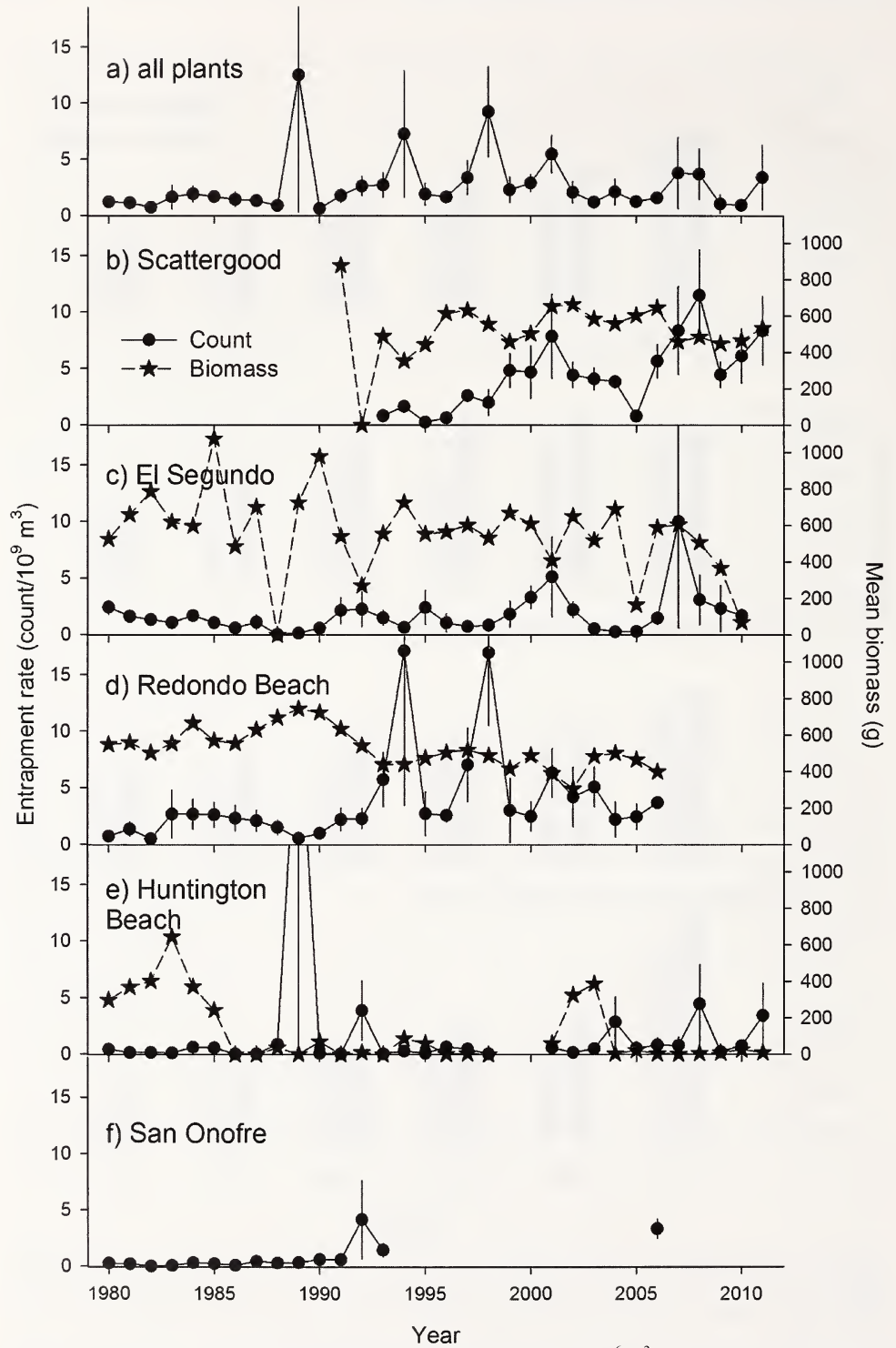


Fig. 5. Mean annual California spiny lobster entrapment rate (count/10⁶ m³) at a) all plants combined, b) Scattergood (1993–2011), c) El Segundo (1980–2010), d) Redondo Beach (1980–2006), e) Huntington Beach (1980–1998, 2001–2011), and f) San Onofre (1980–1993, 2006). Mean biomass (g) per individual lobster for b, c, d, and e by year derived from total abundance/total biomass, not individual weights. Therefore, no measure of variation around the mean.

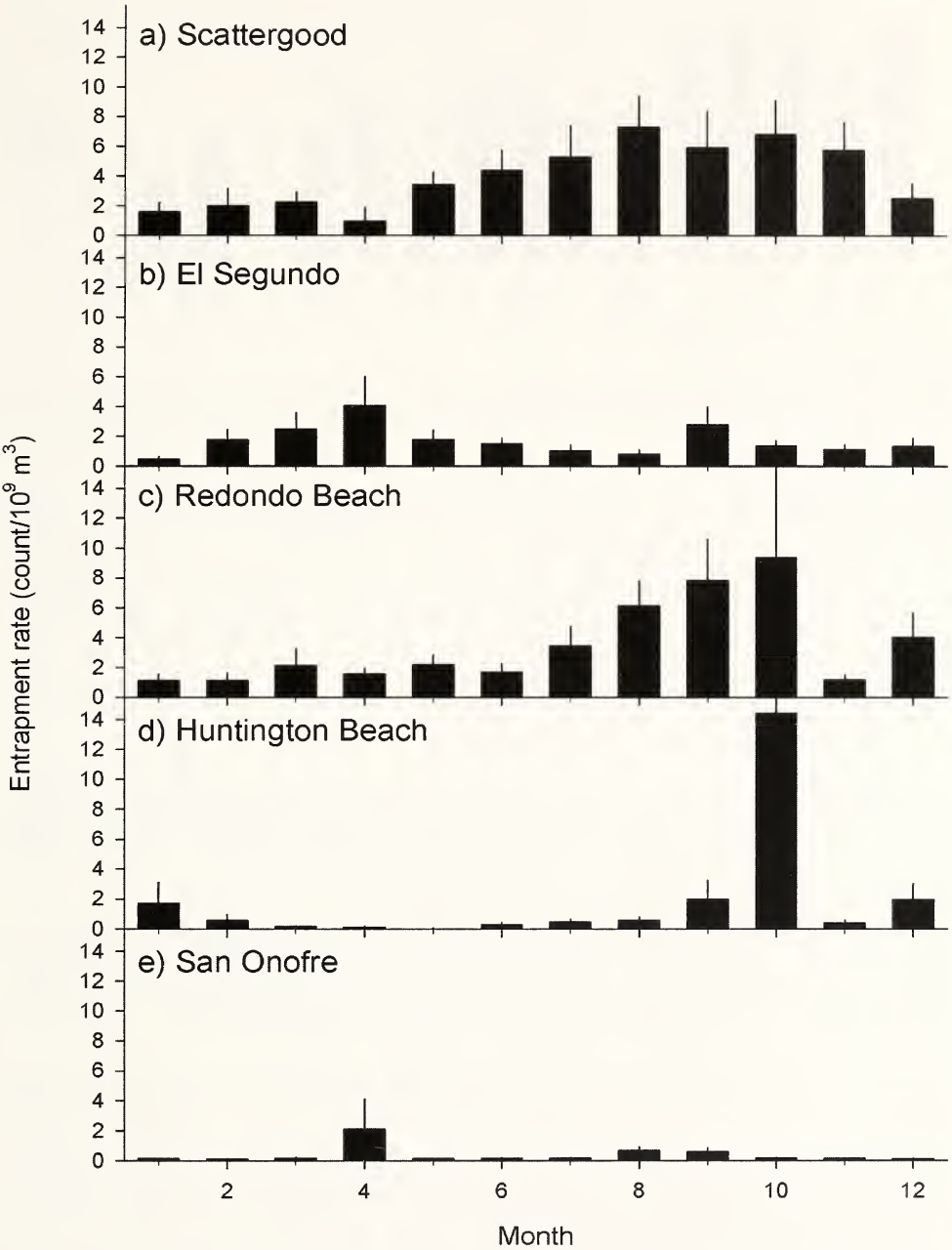


Fig. 6. Mean monthly California spiny lobster entrapment rate (count/10⁶ m³) at each of the five power plants: a) Scattergood (1993–2011), b) El Segundo (1980–2010), c) Redondo Beach (1980–2006), d) Huntington Beach (1980–1998, 2001–2011), and e) San Onofre (1980–1993, 2006).

small CL was consistent with the trends in biomass and the sporadic high ERs recorded. Prior to 1989, the mean lobster weighed 388 g but declined after 1988 to 9 g. In 1989, the most abundant year at HBGS, the mean individual biomass was 1 g.

Comparatively minimal data was available from SONGS, but those data indicated a consistently low ER through 1991 before increasing in 1992 to 4 lobster/10⁹ m³ and

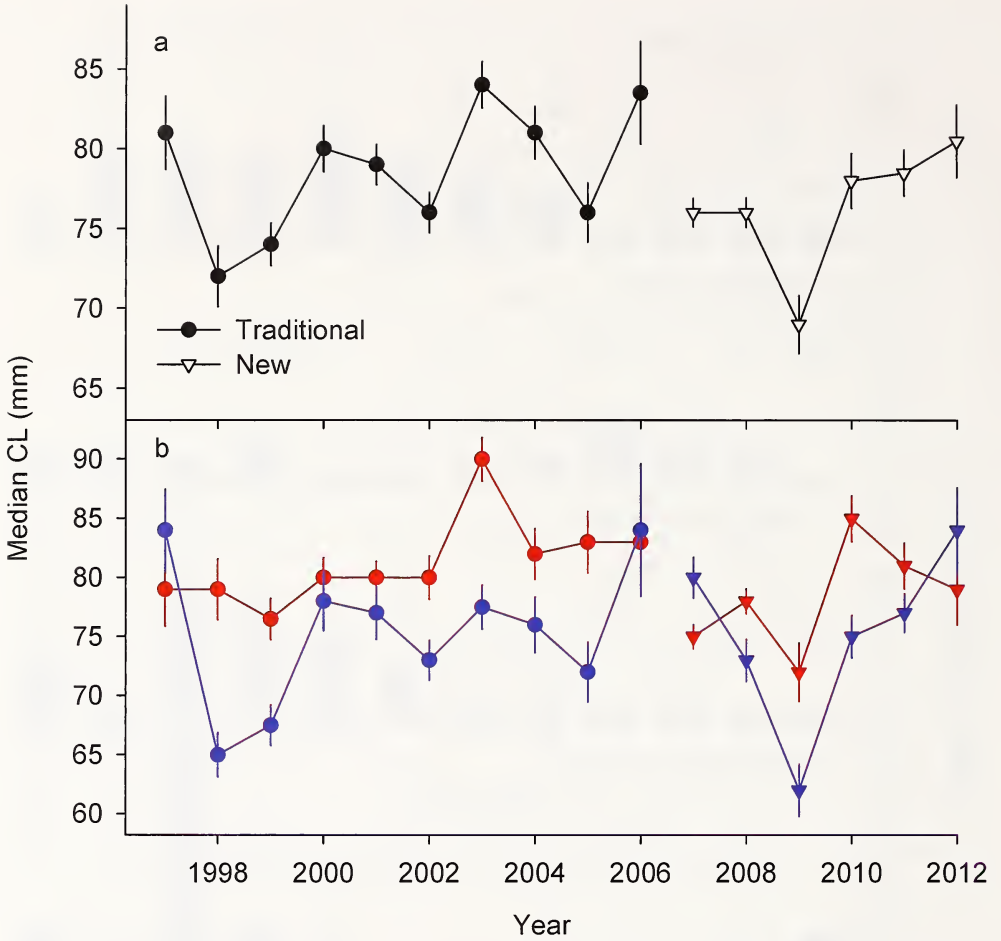


Fig. 7. Median ($\pm$ s.e.) California spiny lobster carapace length (mm) of lobsters taken during power plant surveys at Scattergood (1998–2012) divided by periods where the traditional hoop net (Traditional) and new hoop net (New) were used for all lobsters a) combined and b) by sex (female in red, male in blue). Data was adjusted to correspond to California spiny lobster fishing seasons, October 1 - September 30. For example, October 1, 2009 - September 30, 2010 = 2009.

remaining above 1 lobster/ 10^9 m^3 in 1993 when lobster entrapment monitoring stopped (Figure 5f). A special study in 2006 recorded 3 lobster/ 10^9 m^3 , consistent with the remaining plants in a higher ER recorded recently in comparison to annual mean ERs prior to 1989. The median CL for lobsters collected at SONGS was 66 mm or similar to all other sites except HBGS (Table 2).

The annual NYFI trend was insignificant, but several well-above average recruitment events occurred since 1993 (Figure 3a). Large recruitment events in 2001 and 2008 were especially noteworthy as they stood out considerably from the remaining years. This corresponded to the period of increasing and stable commercial landings. The commercial landings were successfully predicted by the NYFI in a sigmoidal regression: $\text{Landings} = 266.9/(1+\exp(-(\text{NYFI}-54.5)/235.1))$ ($r^2 = 0.50$, $p = 0.02$; Figure 3c). The sigmoidal curve reached an asymptote at an $\text{NYFI} = 1000/10^9 \text{ m}^3$ as commercial landings were consistently between 250 and 265 MT in years with an $\text{NYFI} > 1000/10^9 \text{ m}^3$. Therefore the NYFI was subsampled to include only years with $< 1000/10^9 \text{ m}^3$

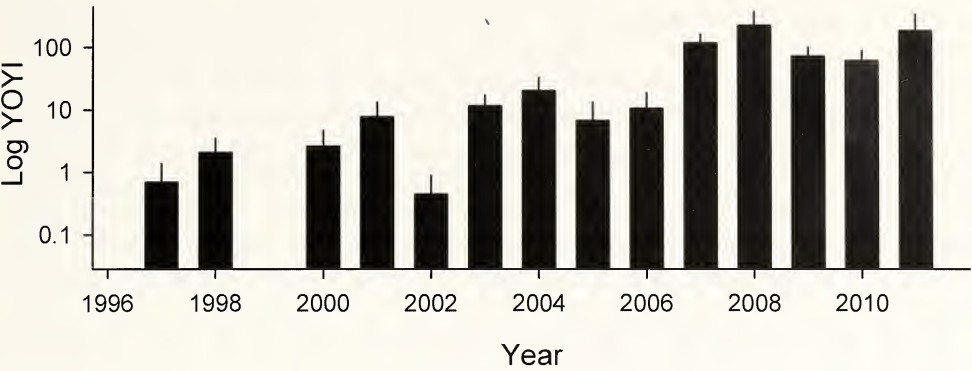


Fig. 8. The mean annual (1993–2011) California spiny lobster young-of-the-year index (YOYI) plotted on a log scale. Data drawn from surveys at Scattergood, El Segundo, Redondo Beach, and Huntington Beach.

(Figure 3d). Greater landings predictability was achieved ($r^2 = 0.57$, $p < 0.001$) using the linear relationship $L = 0.16 \cdot \text{NYFI} + 136.2$. Derived through similar methods as the NYFI, beginning in 1992 when measurements started, the YOYI indicated minimal larval settlement until 1997 (Figure 8). Since 1997, young-of-the-year lobsters were entrapped every year with the exception of 1999. When adjusted for autocorrelation in both the YOYI and NPGO, no significant correlation was detected with any of the environmental indices (Table 3).

Discussion

Spiny lobsters are prized marine species targeted chiefly by commercial fishing interests throughout their global range (Phillips 2006). In many cases, the local spiny lobster fishery ranks among the most valuable fisheries in the area due to the high price per kg. This value leads to extensive interest in achieving a sustainable fishery, often through intensive monitoring and fishery investigations (Pringle 1986; Cruz et al., 1995; Acosta et al., 1997; Cruz and Adriano 2001; Eggleston et al., 2003; Phillips et al., 2005; Phillips and Melville-Smith 2005; Arteaga-Ríos et al., 2007; Parnell et al., 2007; Neilson et al., 2009; Phillips et al., 2010; Miller et al., 2011a; Kay et al., 2012b). Despite its prominence in California’s commercial fisheries (Mitchell et al., 1969; Barsky 2001), few studies examined the lobster population and fishery in California to adequately inform management. The need for fishery-independent population data, especially for pre-recruit age

Table 3. Spearman rank correlation results for tests between California spiny lobster young-of-the-year index and each climate/oceanographic index. Indices tested include North Pacific Gyre Oscillation (NPGO), Coastal Upwelling Index (CUI), Pacific Decadal Oscillation (PDO), Multivariate ENSO Index (MEI), and bottom sea temperature (BST). Autocorrelation test results using a Durbin-Watson test (DW) are presented in addition to the r_{crit} derived in cases where autocorrelation were detected in either the climate/oceanographic or lobster abundance index.

Index	DW	DW p	r	p	r_{crit}
NPGO	0.58	<0.01	0.49	0.03	0.79
CUI	1.79	0.21	0.02	0.94	0.68
PDO	1.44	0.03	−0.48	0.03	0.68
MEI	1.67	0.13	−0.33	0.15	0.68
BST	1.47	0.04	−0.27	0.24	0.68

and size classes, was recently outlined (Cope et al., 2011). Without such data, fishery managers were forced to rely on landings information and other fishery-dependent data, which can lead to a misrepresentation of the population status (Erisman et al., 2011).

Seeing these gaps, a review of both fishery data and a novel power plant time series was executed to try and gain a greater understanding of the populations. Several points, discussed in greater detail below, became apparent. These included: 1) landings steadily increased in recent decades, but the associated effort was undocumented; 2) regulatory concerns over the new hoop net design were likely warranted; 3) timing of the 1980s increase in the lobster population and subsequent landings coincided with the 1989 oceanographic regime shift; and 4) no evidence was found linking the recent increase in southern California lobster landings to currently-available and commonly used climate indices.

Commercial fishing harvested lobsters from throughout the Southern California Bight, but the majority of the landings were reportedly taken from fishing blocks offshore Los Angeles County and south. Along the mainland coast, prominent rocky headlands such as Palos Verdes in Los Angeles County, Dana Point in Orange County, and Point Loma in San Diego County contributed the majority of lobster landings over time although the fishery expanded north in later years. These patterns may be artifacts of effort distribution. In the absence of effort data, this cannot be ruled out. It stands to reason, however, that areas where lobsters have been caught before were likely targeted again.

Notable areas without any reported commercial landings include the leeward side of Santa Catalina Island and within the Santa Monica Bay, both areas where commercial lobster fishing was prohibited. During the 2010–11 season, the third through fifth highest ranked sites for recreational lobster catch (35,356 lobsters reportedly caught) were within or near Santa Monica Bay (California Department of Fish and Wildlife 2012). Santa Catalina Island ranked first, although no information on location was included to place the catches in or out of areas closed to commercial fishing. Fishery-independent data was robust in the Santa Monica Bay due to the presence of three monitored power plants. Each recorded stable to increasing abundance indices, although two of the series terminated prematurely due to vagaries in the electricity generation industry.

The third Santa Monica Bay power plant, SGS, provided robust data during most of the population rise and recorded the only meaningful positive trend in abundance. Lobsters collected at SGS were near the minimum size for the fishery, but a significant decrease in the lobster size structure was observed between 2006 and 2007. The significant difference between the pre-2007 and post-2006 periods was represented in the combined sample across both sexes and for females; no significant difference was detected in males. Spiny lobsters execute seasonal movements, typically onshore offshore timed with changes in water temperature (Mitchell et al., 1969; Kanciruk and Herrnkind 1978), but no longshore migration has thus far been reported for lobsters after settling from the plankton. The lack of robust size and catch information from the recreational fishery precluded any clear conclusions, but the reduction in size in an area free of commercial fishing pressure was cause for concern. This was especially disconcerting given the significant change in females. Increasing evidence suggests losses of bigger and older females severely impacts fisheries well beyond losses of smaller, younger females due to the exponentially higher fecundity and genetic makeup associated with attaining old age and large size (Berkeley et al., 2004a; Berkeley et al., 2004b; Birkeland and Dayton 2005). Furthermore, the timing of the downsizing lends more circumstantial evidence suggesting an effect of the new hoop net. More data is needed to verify this impact, but the present

data should elicit cautionary management practices to protect the resource while additional data is acquired.

Regardless of the spatial distribution in catch, sustained, elevated landings throughout the 2000s were assumed to reflect a sustainable fishery (Neilson 2011). These patterns, however, belie potential pitfalls in the future related to variable fishing effort (and efficiency) and environmental forcing. While insufficient data existed to conclusively determine an impact, the introduction of the new hoop net and its increasing use (Neilson and Buck 2008) appeared to impact the commercial fishery and population at large. This was consistent with comments of commercial fishers, who claimed to catch fewer lobsters with more effort (Neilson 2011). In itself, a redistribution of harvest between the recreational and commercial interests may not be cause for alarm. It does, however, indicate that the recreational harvest may be substantial and warrants careful consideration in management actions. The declining size collected at SGS should be cause for alarm and investigation. Unfortunately, insufficient data exists on the scope of the recreational fishery, especially core parameters such as the number of active participants and some measure of their annual catch and size structure to support a clear conclusion on this matter. Examination of the recreational harvest effects during a recreational-only mini season in Florida for *Panulirus argus*, similar to the mini season for California spiny lobster in California, indicated substantial reductions in the local, legal-sized population prior to the opening of the commercial fishery (Eggleston et al., 2003).

Like many fish species, lobster abundances and fishery were robust when strong larval settlement and subsequent recruitment occurs (Beaugrand et al., 2003; Beaugrand and Kirby 2010), such as the latter period for lobster in southern California. Harvest pressure from commercial and recreational interests during periods of declining settlement can quickly lead to overfishing, e.g. *Gadus morhua* (Beaugrand et al., 2003; Beaugrand and Kirby 2010). Such was the case in the Hawaiian spiny lobster fishery in the Northwest Hawaiian Islands where recruitment declined 47% after 1989 without an accompanying decline in fishing effort eventually leading to a fishery collapse (Polovina et al., 1995; Polovina 2005). While lacking any statistical link between the climate indices tested and either population or fishery abundance indices, the timing of changes in California's spiny lobster populations were highly coincidental with the documented 1989 regime shift. The 1989 regime shift resulted in substantial changes to the Southern California Bight coastal fish populations with a similar lack of correlation with common climate indices (Miller and McGowan 2013). Polovina (2005) hypothesized the shift altered current patterns in the waters surrounding the Hawaiian Archipelago resulting in decreased productivity and, perhaps more importantly, disrupted larval dispersal and delivery patterns. Both the California and Hawaiian spiny lobsters pass through a lengthy larval phase with their larval drift predicated on local currents. Growing genetic evidence suggested changes in long-held beliefs of larval supply to southern California from Baja California was warranted, such that the local populations may be self-supporting (Selkoe et al., 2006; Selkoe et al., 2007; Selkoe et al., 2010; Iacchei et al. 2013). Given the 1989 shift appeared to be a Pacific-basin wide phenomena, a similar shift in current patterns within the Southern California Bight likely occurred to the benefit of the local lobster population.

Perhaps the strongest indication of a positive shift in lobster settlement in the late-1980s was recorded in the power plant monitoring. This was especially true at HBGS where after two years of no lobsters recorded (1987–88), the highest ER occurred in 1989. Unlike previous years, the average lobster weighed approximately 1 g (695 lobsters

weighing 777 g). In 16 of the following 19 years of monitoring (no surveys in 1999–2000) where the ER was ≥ 1 , the average lobster weighed less than 10 g 50% of the time. A similar, albeit less demonstrative, shift towards smaller individuals was recorded at the remaining power plants. The location of the HBGS intake likely made it an effective puerulus/juvenile lobster collector. Situated offshore of sandy beaches along an extensive stretch of soft-bottom habitat, the HBGS intake structure and surrounding riprap represented one of the few suitable habitats in the immediate area for puerulus to settle out of the plankton. Abundances of settling *Jasus verreauxi* in collectors placed over sandy bottom habitat offshore from natural habitat known to attract settlers was significantly higher than those placed near preferred natural habitats (Montgomery 2000). While both SGS and ESGS were both located in similar habitat, neither recorded the level of larval settlement observed at HBGS. Lacking additional information, no hypothesis can be presented for this difference at this time. Nevertheless, this warrants further investigation incorporating time series data on current patterns and productivity in the Southern California Bight, similar to that completed for the Hawaiian Archipelago (Polovina et al. 1993; Polovina et al. 2005).

This apparent pattern of increasing settlement likely led to the continually high landings in the commercial fishery over the last decade. The increasing strength of the YOYI suggests the population will continue to support a robust harvest in the near term. Deriving a maximum sustainable yield for the combined fisheries (commercial and recreational), however, remains an unsettled matter. Given the size classes targeted by each fishery, the commercial landings will likely decline earlier than the recreational fishery. Designing traps to preferentially target new recruits minimizes the impact of taking larger, more fecund females. This practice has more potential to result in a sustainable fishery in comparison to those that target larger, trophy individuals (Berkeley et al., 2004a; Berkeley et al., 2004b; Birkeland and Dayton 2005). Reliance on one or two recently-recruited year classes, however, renders the commercial fishery more susceptible to recruitment failure than the recreational fishery. Fishing equipment available to the recreational fishery does not suffer such size selectivity.

Conclusion

The fisheries were clearly landing high biomass (in comparison to the 1980s) as recently as 2010, the last year of fishery data included in this study. Reasons for concern were present that warranted further investigation. Specifically, the introduction and use of a new hoop net in the recreational fishery raised concern. While the commercial fishery was extensively regulated as a limited entry fishery supplying catch statistics each calendar year, the recreational fishery required only a fishing license with, until 2008, no requirement to report catch statistics. Prior attempts to examine the lobster population and fisheries were impacted by the limited availability of fishery-independent data. Utilizing novel data collected at local power plants assisted with this evaluation. These data suggested the lobster population was more robust in recent decades than during the 1980s due to increased larval settlement. Mean lobster weight indicated increased larval settlement in the area beginning in 1989, coincidental with the timing of an oceanographic regime shift to one promoting lobster settlement in southern California. These data and analyses all indicate that while the lobster fishery in southern California appears healthy at the moment, it warrants careful management in the face of variable ocean conditions. Most pressing was the need to better monitor and document the recreational fishery and monitor sublegal size classes from larval settlement through fishery recruitment.

Acknowledgements

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Black Bears (*Ursus americanus*) as a Novel Potential Predator of Agassiz's Desert Tortoises (*Gopherus agassizii*) at a California Wind Energy Facility

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Areas of significant topographic relief often form ecoclines, resulting in stratified life zones each with distinct communities of plants and animals (Attrill and Rundle 2002). Contact zones, or ecological boundaries along ecoclines, allow unique plant and animal assemblages that are not normally considered to be syntopic, to mix in varying degrees. The boundaries of ecoclines are thus both spatial and ecological and when these boundaries are crossed unique interactions can occur, including unexpected predator and prey interactions.

The eastern San Bernardino Mountains in southern California range from about 300–3,506 m and support a wide range of as many as 11 distinct life zones along an ecocline extending from Sonoran Desert on the east side and Mojave Desert on the north side, to an alpine ecosystem near the summit (Schoenherr 1992). In this paper we report an interaction between black bears (*Ursus americanus*) and Agassiz's desert tortoises (*Gopherus agassizii*). These two species have not previously been reported to interact due to their substantially different habitat preferences. In addition, given the paucity of bear and turtle interactions in general, we provide a review of the scientific literature on the topic, since bears are known to eat turtles on an opportunistic basis.

The study site is located in the foothills of the southeastern San Bernardino Mountains in Riverside County, California, near the city of Palm Springs (33°57'06"N, 116°40'02"W, WGS84). Known locally as "Mesa," the site is located on land administered by the Bureau of Land Management for wind energy generation since 1983. Extensive studies of *G. agassizii* have been conducted at the site since 1994, including investigations on growth, demography and survivorship (Lovich et al. 2011b), fire ecology (Lovich et al. 2011c), habitat selection (Lovich and Daniels 2000), the effects of climate on behavior and reproductive ecology (Ennen et al. 2012b; Lovich et al. 2012; Lovich et al. 1999), nesting ecology (Ennen et al. 2012a) and the impacts of wind energy operation and maintenance on tortoises (Lovich and Ennen 2013; Lovich et al. 2011a).

Mesa is at the extreme western edge of the Lower Colorado River Subdivision of the Sonoran Desert ecosystem, commonly referred to as the "Colorado Desert" (Turner and Brown 1994). Because of its location near several major ecosystems, vegetation at the site

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Fig. 1. Example of a Reconyx trail camera setup at an active Agassiz's desert tortoise (*Gopherus agassizii*) burrow in the San Bernardino Mountains northwest of Palm Springs, California in 2013. Cameras were attached to fence posts within 1–2 m of burrows and would trigger on wildlife activity.

is a mixture of species from the Mojave and Sonoran deserts as well as cis- and trans-montane (sensu Schoenherr 1992) chaparral and coastal sage scrub plants. Anthropogenic features include 460 wind turbines and an infrastructure of dirt roads, transformers, a substation, and a maintenance shop staffed on weekdays. More detailed descriptions of the study site are given by Lovich and Daniels (2000) and Lovich et al. (2012).

During the summer of 2013, 37 Reconyx trail cameras (models HC500 and PC800) were deployed at *G. agassizii* and California ground squirrel (*Otospermophilus beecheyi*) burrows as part of an ongoing study to investigate the effects of noise and vibration on these species. Cameras were programmed to take five high definition photographs when triggered (0.2 sec trigger speed) by wildlife activity and were positioned 1–2 m from burrow entrances (Figure 1). Cameras were checked monthly for wildlife photos. In addition, 14 *G. agassizii* were fitted with radio transmitters as part of ongoing research on the fire ecology and reproductive biology of the species (Lovich et al. 2011c). Tortoises were located at approximately 10 day intervals from April–July, 2013 and females were X-radiographed (Hinton et al. 1997) to determine gravidity, clutch size and clutch frequency (Lovich et al. 2012).

On June 22, 2013, starting at 0050 h, we recorded a series of 28 photographs showing a female black bear and at least one cub at the entrance to a tortoise burrow. The female directly faced the opening of the burrow in one photograph (Figure 2) as if smelling its occupant(s). In another photograph, the cub was looking at the burrow (Figure 3). The bears were not observed digging in the photos. On that date we suspected that there was at least one female tortoise in the burrow (based on radio-telemetry and trail camera monitoring), but two males were known to have visited and co-occupied that burrow four times during the spring and summer of 2013. It is not unlikely that two or more tortoises were in the burrow at the time it was investigated by the bears. One male tortoise was verified as a co-occupant of the burrow on July 19.



Fig. 2. An adult female black bear (*Ursus americanus*) investigating an occupied Agassiz's desert tortoise (*Gopherus agassizii*) burrow in the San Bernardino Mountains near Palm Springs, California. The site is an active wind energy generation facility. Date and time stamps of the wildlife trail camera are shown at the top of the image along with air temperature.

The burrow, about 3 m in length, has been used regularly by the same female from 2009–2013. Female tortoises at this site deposit clutches of eggs in or near the burrow entrance (Ennen et al. 2012a), but the only female that uses the burrow visited by the bears has never produced a clutch of shelled eggs since monitoring began in 1997 (Lovich et al. 1999). It is thus unlikely that tortoise eggs were in the burrow entrance at the time it was visited by the bears. The last bear photo was taken at 0051 h on June 22, 2013. No evidence of digging by bears was observed on subsequent visits to the burrow by researchers during the remainder of the field season (last visit November 14, 2013).

Black bears occupy an astonishing diversity of habitats across their range in North America, from tundra to the edge of desert ecosystems, because of their ecological plasticity (Stirling and Derocher 1990). Despite this broad range of habitats, they are generally fond of treed areas, especially when found with grizzly bears (*Ursus arctos*) (Herrero 1972), and this is mirrored in their California distribution (Brown et al. 2009). In the San Bernardino Mountains black bears occupy a similarly broad range of habitats but prefer montane forests with a wide variety of seral stages (Novick and Stewart 1982; Stephenson and Calcarone 1999). Bears do occasionally move down into the desert from the San Bernardino Mountains as confirmed by Burghdoff (1935), occasional newspaper reports, rare sightings by Mesa maintenance staff, and a bear sighting in nearby Big Morongo Canyon on 27 July, 1993 by one of the authors (JEL). However, the xeric habitat types occupied by tortoises render expected encounters by these two species occasional at best. The “Hathaway Fire” that burned near Banning, California from 9–20 June, 2013, about 13 km northwest of our study site, may have pushed the bears into our study area from occupied habitat (Novick and Stewart 1982). Fire and fire management have dramatic impacts on bears and their habitat (Mattson 1990).

Black bears in California, including those in the San Bernardino and nearby San Gabriel Mountains of California, subsist largely on herbaceous plant material and acorns



Fig. 3. A black bear (*Ursus americanus*) cub investigating an occupied Agassiz's desert tortoise (*Gopherus agassizii*) burrow in the San Bernardino Mountains near Palm Springs, California. The cub's mother was nearby (see Figure 2). The site is an active wind energy generation facility. Date and time stamps of the wildlife trail camera are shown at the top of the image along with air temperature.

in the spring, fruit and acorns in the summer, and fruit, acorns and other nuts in the fall (Boyer 1976; Stubblefield 1993). Although we did not observe a predatory event *per se*, the omnivorous diet of bears (including black bears) does include turtles (Table 1), so the potential exists for predatory encounters when the species meet. Comparatively few publications document turtle predation by bears and none document predation on *G. agassizii*. The earliest published record we found of bears eating turtles was Romans (1775 (a facsimile reproduction, 1962)) account of “droves” of black bears coming down to Florida beaches to eat the eggs of nesting loggerhead sea turtles (*Caretta caretta*). In their review of the ecology of turtles of the United States and Canada, Ernst and Lovich (2009) reported that bears are included in the list of predators of turtles or their eggs for loggerhead sea turtles (as cited by Dodd, 1988 who, in turn, cited Romans, 1775), common snapping turtles (*Chelydra serpentina*), western pond turtles (*Actinemys marmorata*; see also Vander Haegen et al., 2009), peninsula cooters (*Pseudemys peninsularis*), and Florida softshell turtles (*Apalone ferox*). Behrend and Sage (1974) observed an adult snapping turtle that they presumed to be a nesting female shortly after it was killed and partially consumed by a black bear, leaving only one egg and various body parts.

Turtle predation is not limited to black bears. Krofel (2012) found a Hermann's tortoise (*Testudo hermanni*) in northern Greece that appeared to have been killed by a brown bear (*Ursus arctos*). Krofel then used the percentage of brown bear scats reported by Paralikiidis (2010) from northern Greece that contained unspecified turtle remains to estimate that around 28,000 tortoises could be consumed by the brown bear population in his study region annually. The diet of Malayan sun bears (*Helarctos malayanus*) in Malaysian Borneo also included turtles such as the Asian brown giant tortoise (*Manouria emys*). Turtle remains occurred in 5.77% of the sun bear scats examined (Wong 2002).

Table 1. Published records for bear predation, or possible predation, on various turtles. The reader is referred to Ernst and Lovich (2009) for additional primary literature citations for species listed below other than those given here.

Bear species	Turtle species	Location	Citation
<i>Helarctos malayanus</i>	<i>Manouria emys</i>	Malaysian Borneo	Wong et al. (2002)
<i>Ursus americanus</i>	<i>Caretta caretta</i>	USA	Ernst and Lovich (2009)
<i>Ursus americanus</i>	<i>Chelydra serpentina</i>	USA	Behrend and Sage (1974), Ernst and Lovich (2009)
<i>Ursus americanus</i>	<i>Actinemys marmorata</i>	USA	Holland (1994), Ernst and Lovich (2009)
<i>Ursus americanus</i>	<i>Pseudemys floridana</i> (= <i>P. f. concinna</i>)	USA	Thomas and Jansen (2006)
<i>Ursus americanus</i>	<i>Pseudemys peninsularis</i>	USA	Ernst and Lovich (2009)
<i>Ursus americanus</i>	<i>Apalone ferox</i>	USA	Pope (1939), Ernst and Lovich (2009)
<i>Ursus arctos</i>	<i>Testudo hermanni</i> and others	northern Greece	Krofel (2012)
<i>Ursus arctos</i>	Unspecified	western Greece	Paralikidis et al. (2010)

Agassiz’s desert tortoises have a large number of predators including other medium to large mammals like mountain lions (*Felis concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and domestic dogs (*Canis familiaris*) (Ernst and Lovich 2009). All of these predators are also present at or near our Mesa study site. Given our observation of bears at the study site, there is a risk of predation on desert tortoises by this potentially novel predator. The probability of bear predation is very likely low due to minimal range and habitat overlap between the species and the fact that California black bears have a diet dominated by plant material (Boyer 1976; Stubblefield 1993). However, the fact that turtles are included in the diets of bears worldwide supports the possibility that it can occur. Bears are known for developing unique foraging behaviors through learning so it is possible that individual bears might develop a preference for tortoises if given the opportunity (Stirling and Derocher 1990). Krofel (2012) suggested that predation and partial consumption of tortoises was a learned behavior and that some bears could become specialized tortoise eaters.

It is unlikely that *G. agassizii* experienced predation by black bears in historical times, especially since the latter were not native to southern California during that time period. Indeed, we found no published evidence to support such an interaction. Grizzly bears (*Ursus arctos horribilis*) were the only bears in central coastal and southern California just prior to European colonization (Brown et al. 2009). Although *U. arctos* are known to eat different tortoise species elsewhere in the world (Krofel 2012; Paralikidis et al. 2010), we could find no evidence that they ate *G. agassizii*. Following the extirpation of grizzly bears in California ca. 1920 (Mattson and Merrill 2002), 16 black bears from the Sierra Nevada near Yosemite were released in the San Bernardino Mountains in 1933 (Burghduff 1935), an event still reflected in their genotypes (Brown et al. 2009). Thus black bears in southern California are an introduced species and tortoises may not be well-adapted to possible predation by that species.

Even a single individual of a novel predator can have significant effects on small populations of Agassiz’s desert tortoises. An example was provided by Medica and Greger (2009) who recorded a mortality event attributed to a mountain lion (*Felis concolor*) that killed eight *G. agassizii* at a Mojave Desert study site in southern Nevada in

2003. This predation event was the first observed during their 45 year study. The authors suggested that this was an example of a learned behavior in a mountain lion passing through low elevation, normally unsuitable Mojave Desert habitat in late summer or early fall. Although mountain lions and jaguars (*Panthera onca*) are known predators of various tortoise species in the Western Hemisphere (Averill-Murray et al. 2002; Emmons 1989) including other desert tortoises (*G. morafkai*), published instances of big cats feeding on tortoises appear to be as rare as those involving bears and tortoises. However, if a single black bear developed a taste for tortoises, it could have negative effects on a small population of desert tortoises similar to what was observed by Medica and Greger as a result of mountain lion predation. A single adult tortoise can “easily” satisfy the estimated daily food requirements of a large predator like a jaguar (Emmons 1989), so it would be energetically advantageous for black bears to eat tortoises when they are encountered.

If tortoise predation is eventually practiced by black bears at our Mesa study site, it could have negative effects on the small resident tortoise population (Lovich et al. 2011b). Researchers and resource managers need to be aware of the potential for novel introduced predators like black bears to affect federally threatened species like *G. agassizii*.

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Flight Initiation Distance Differs between Populations of Western Fence Lizards (*Sceloporus occidentalis*) at a Rural and an Urban Site

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For a given animal, life consists of a series of decisions and compromises made in an effort to maximize fitness. These include decisions about how much time and energy to apportion to foraging, reproduction and associated social activities, and when to abandon these resources in the presence of a predator. The decision of when to flee is critical to the fitness of an individual (Cooper and Whiting 2007). According to escape theory, there is a balance between the cost of fleeing and the chance of being caught (Dill 1974); this tradeoff results in a decision as to how close a predator should be permitted to approach before initiating flight behavior (i.e., flight initiation distance; Ydenberg and Dill 1986, Cooper and Frederick 2007). Furthermore, there is a tradeoff between the antipredator behaviors of crypsis and flight; namely, when an animal initiates flight, it increases its likelihood of being detected by the predator (Martín et al. 2009).

Flight initiation distance (FID) is a trait that varies between populations and can be affected by factors including vegetation cover, type of predator, and predator density and efficiency (Blázquez et al. 1997, Diego-Rasilla 2003, Camp et al. 2012). Flight initiation distance has been studied in lizards extensively (e.g., Cooper and Whiting 2007, Martín et al. 2009, Cooper 2010, Cooper 2011). Generally, in populations exposed to higher predator densities, lizards are more wary and display longer FIDs (Diego-Rasilla 2003); that is to say, they initiate flight behavior while the predator is farther away, as compared to those in environments with lower predator densities.

In many animals, predation response is specialized (e.g., Walther 1969, Ghalambor and Martin 2000). The Western fence lizard (*Sceloporus occidentalis*) can distinguish between potential predators using visual cues about size and movement patterns (Fitch 1940, Fine 1999). This small, primarily insectivorous lizard is ubiquitous in open, sunny habitats west of the Rocky Mountains (Stebbins 2003). Common predators of this widespread species include snakes (e.g., racers, kingsnakes; Fitch 1940), mammals (e.g., foxes, raccoons, shrews; Nussbaum et al. 1983), and birds (e.g., kestrels, shrikes; Fitch 1940, Cooper and Whiting 2007). While encounters with humans may result in the occasional removal of an individual from a population (e.g., collection for the pet trade or incidental death), humans do not generally play the role of predator for Western fence lizards. Consequently, at sites with regular human activity these lizards should not view humans as dangerous predators and FID in response to humans should be reduced. Since flight for FID studies is usually initiated by a human researcher, it would be useful to determine if lizard FID responses differ between populations exposed to different human densities. This information would determine if it is necessary to choose study sites with similar human activity levels in order to remove unnecessary site bias from a study. We measured the flight initiation distances of lizards from two populations of Western fence lizards with different human exposure to determine if there was a difference in FID between the

two. Based on escape theory, we predicted that FID would vary with the population's exposure to human presence.

We conducted our study along fence lines at Snobird Lane in the San Luis National Wildlife Refuge, Merced Co., California (rural site), and at Taylor Road in Turlock, Stanislaus Co., California (urban site) during April-June, 2013. The rural site consisted of 763-m of barbed wire fence line along a dirt road separating an active almond orchard and the cattle-grazed grasslands of the wildlife refuge. This dirt road connects to a two-lane highway and serves as an access point to the refuge. Dense vegetation was available for cover around and between fence posts. The urban site consisted of 1150-m of concrete wall located along a sidewalk with regular foot traffic separating an urban residential area and an irrigation canal paralleling Taylor Road. Taylor Road is a busy two-lane street bordering farm land. We conducted our study on the foot path along the heavily vegetated side of the wall.

Each site was visited three times, and temperature, cloud cover, and wind speed were recorded. All observations were made in temperatures ranging between 25.6–35.2°C. On each sample day, we slowly walked the fence line searching for Western fence lizards. Once we observed a lizard, one observer walked slowly toward it until the lizard fled. If the lizard did not flee by the time the observer was directly in front of it, the observer left the path and directly approached the lizard until it fled. Flight initiation distance, the straight line distance between the researcher and the lizard's initial position, was measured using a laser rangefinder (Leica DISTO E7400x, Leica Geosystems, Heerbrugg, Switzerland). To avoid pseudoreplication, we only recorded FIDs of Western fence lizards encountered while walking in one direction along the fence line. In order to assess potential predation threats at each site, we also recorded all observations of predatory birds near enough to be reliably identified. Because the FID data were not normally distributed and transformations did not correct this problem, we used a nonparametric Mann-Whitney U test (SPSS 21, IBM Corporation, Armonk, USA) to test for a difference in FID between the two study sites. We used a Student's t-test (SPSS 21, IBM Corporation, Armonk, USA) to determine whether the abundance of predatory birds differed between the two sites.

We measured FID for 29 lizards at the rural site and for 65 lizards at the urban site. The Western fence lizards observed included males and females ranging from subadult to adult at each study site. At the rural site the average FID was 9.69-m (range: 1.35–30.45-m). At the urban site the average FID was 3.57-m (range: 1.02–8.38-m; Figure 1). Western fence lizards at the rural site initiated flight at a significantly longer distance than those at the urban site ($z = -3.44$, $df = 102$, $p < 0.001$). Predatory birds were significantly more abundant at the rural site ($t = 1.443$, $df = 5$, $p = 0.027$), where an average of 5.2 predatory birds were observed per hour (range: 1.30–12.3 birds/hr). At the urban site, there was an average of 0.5 predatory birds observed per hour (range: 0–0.8 birds/hr).

Many factors can influence FID, and lizards in areas with substantially different environments would be expected to exhibit different levels of wariness (e.g., Cooper and Whiting 2007, Camp et al. 2012). In this study, FID was found to differ significantly between study sites, with lizards at the rural site fleeing sooner than those encountered at the urban site. This difference in behavior can be attributed to each population's environment which differed in exposure to people and in predatory bird abundance.

Lizards have the ability to distinguish between potential predators (Fitch 1940, Fine 1999) and animals are known to alter their antipredator responses based on previous experience with that predator (Deecke et al. 2002). Flight initiation distance varied with

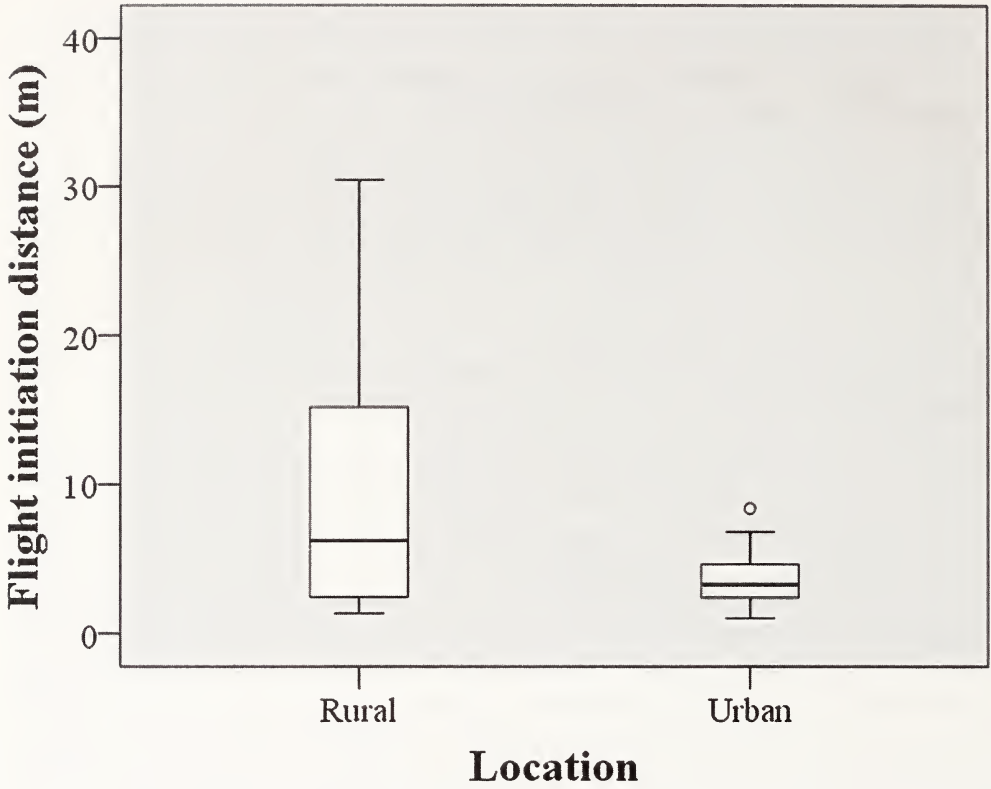


Fig. 1. Western fence lizards (*Sceloporus occidentalis*) at a rural site exhibited significantly higher flight initiation distances ($z=-3.44$, $df=102$, $p<0.001$) compared to urban lizards, and rural site lizards exhibited a wider range of responses. The open dot represents an outlier with a high FID at the urban site.

levels of human use, with lizards at the rural site exhibiting longer FIDs than those at the urban site. At the urban site, there is nearly constant foot traffic along the sidewalk where the lizards were surveyed. These humans generally ignore the lizards and pose little to no threat to the lizards' survival. Following the optimum escape theory, it is expected that lizards that do not view humans as high risk predators would allow humans to approach closer before fleeing than lizards in a naïve population; this behavior allows them to utilize their resources for longer. It follows that the population of lizards at the urban site would have a higher tolerance of humans, which is supported by their shorter FIDs (Figure 1). These results are consistent with studies on other taxa which demonstrate that squirrel (Engelhardt and Weladji 2011) and bird (McGiffin et al. 2013) tolerance of humans varies with level of exposure.

Alternatively, at the rural site, lizards rarely encounter people on foot and so have little individual experience on which to base their decision on when to flee to maximize fitness. With little human traffic, the population would not have been under selection for reduced wariness in response to humans, and without a human-specific antipredator response, the lizards at the rural site must rely on general antipredator responses. According to Dill (1974), prey species have evolved general antipredator responses to stimuli such as approaching objects and loud noises. These responses vary with the intensity of the stimuli following the same risk/economic scale used for recognized predators. Based on this theory, it is predicted that the naïve population would have longer FIDs than the

population with experience of the harmless human stimuli; the population would not have evolved a lack of wariness in the presence of humans. Our data are consistent with this prediction. Furthermore, the greater variance in FIDs at the rural site suggests variation in individual perception of the danger posed by an approaching human; this is also consistent with a population in which the individual experiences of lizards with recognized predators are applied to produce a response to a human model.

The sites also have differences in avian predator abundance which could contribute to the differences in flight initiation observed. Diego-Rasilla (2003) found that predator density affects flight initiation distance in lizards such that lizards under higher predation pressure had greater FID. Our data support this finding, with the more predator-dense rural site having lizards with, on average, longer FIDs. However, this interpretation is tenuous in that only avian predators were recorded in this study. It is likely that other predators were present but not recorded in both the rural and urban sites (e.g., domesticated cats, raccoons, foxes, coyotes).

Flight initiation distances have been found to vary with other environmental factors such as percent vegetation cover (Cooper 2011, Cooper and Whiting 2007). Additional studies would be beneficial to tease out other variables that affect flight initiation distances of the Western fence lizards at these locations. It would be favorable to use several study sites across an urban-rural gradient. Observing lizards in a highly visited rural area, such as a national park, would help in determining which factors contribute most to FID. In addition, it would be useful to determine if there are differences in FID by sex and age. Since Western fence lizards are known to be territorial (Sheldahl and Martins 2000), FID may differ between those who defend their territory or their mates and those who do not. This study is significant in that it demonstrates that FID does differ between the rural and urban sites. Researchers interested in antipredator behavior should select study sites that lack regular human activity or choose methodologies that use a nonhuman model predator in order to collect meaningful data on lizard response.

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